THE CRANIAL OSTEOLOGY OF THE IGUANID LIZARD *STENOCERCUS GUENTHERI* (SQUAMATA: IGUANIDAE) AND ITS POSTEMBRYONIC DEVELOPMENT

by

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ABSTRACT

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In spite of the great diversity of iguanid lizards, detailed descriptions of their osteocrania and postembryonic development are rare. Herein, the adult cranial osteology of the iguanid lizard *Stenocercus guentheri* and its postembryonic development are described based on cleared and double-stained and dry skeletal specimens from a single Ecuadorian population. The amphikinetic skull of *S. guentheri* is short and elevated, and bears teeth on the premaxilla, maxillae, and pterygoids. Mandibular teeth are present on the dentaries. Males having wider skulls than females, no other sexual dimorphism in the cranial osteology was found. Ossification of the articular from Meckel's cartilage, and growth of the parietal (ossification and investment of the frontoparietal fontanelle), are the most significant ontogenetic changes of the splanchnocranium and dermatocranium, respectively. The ossification of the cartilage separating the bones of the braincase is the most relevant postembryonic ontogenetic event of the neurocranium. The number of teeth does not vary ontogenetically and replacement teeth are present throughout postembryonic life. This study includes a list of the osteocranial characters of *Stenocercus* that have been used in systematic studies, as well as a discussion of functional morphology and kinesis.

To Lena

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INTRODUCTION

The first studies on the morphology and development of the lizard skeleton are from the late 19th century (e.g., Cope 1892; Gaupp 1891; Parker, 1880, 1881; Siebenrock, 1892, 1893a,b, 1894, 1895; Versluys, 1898). Beginning with the description of the chondrocranium of *Lacerta agilis* (Gaupp, 1900), the embryonic cranium of the lizard attracted special attention in the early 20th century (e.g., Brock, 1932, 1940; de Beer, 1930; Gaupp, 1906; Pearson, 1921; Rice, 1920). Though literature on the osteocranium of adult lizards is quite extensive, comprehensive, detailed descriptions (e.g., Jollie, 1960; Oelrich, 1956) are scarce. Studies of the development of the cranium of lizards (e.g., de Beer, 1930, 1937; Parker, 1880; Rieppel, 1992a; Sewertzoff, 1900) focus mainly on the chondrocranium (Bellairs and Kamal, 1981). Thus, the morphology and development of the chondrocranium of lizards are the best-studied among reptiles (Bellairs and Kamal, 1981). In contrast, the postembryonic development of the cranium (and postcranium) of lizards is poorly known (e.g., Hikida, 1978; Rieppel, 1984, 1987, 1992b). In an attempt to increase our knowledge of this facet of the osteology of lizards, I describe herein the postnatal development of the osteocranium of the iguanid lizard *Stenocercus guentheri.*

The genus *Stenocercus,* comprising approximately 50 species, is endemic to South America and ranges from northern Colombia to central Argentina (Frost, 1992; Torres-Carvajal, 2000). *Stenocercus* is a member of the large family Iguanidae (Macey et al., 1997) and is presently included in the metataxon Tropidurinae (Schulte et al., 1998). Except for some general taxonomic studies (e.g., Cadle, 1991; Fritts,

1974; Torres-Carvajal, 2000), the systematics of *Stenocercus* has been poorly addressed; as a consequence, the phylogenetic relationships among species of *Stenocercus* have not been ascertained. Hallermann (1994) described the nasal capsules of *S. varius*, but there is no comprehensive description of the morphology and development of the skeleton of any of the species of *Stenocercus*. Nearly all osteological information on *Stenocercus* is contained in comments included in descriptions of characters in systematic studies (Etheridge, 1966; Etheridge and de Queiroz, 1988; Frost, 1992; Frost and Etheridge 1989). Also, Cadle (1991) described briefly a few general features of the skull of five species of *Stenocercus* and discussed the pterygoid teeth in some species. The following account provides a detailed description of the osteocranium of *S. guentheri*, along with its postembryonic development. This study will facilitate identification of informative characters of cranial morphology that can be used to infer the phylogenetic relationships among members of the genus *Stenocercus*.

MATERIALS AND METHODS

Eighteen post-hatchling specimens of *Stenocercus guentheri,* having snout-vent lengths (SVL) of 30–88 mm, were examined (Table 1). Size is not an accurate estimate of age in reptiles (Andrews, 1982); nonetheless, size was the only available criterion for selecting the specimens. Although the neonatal size of *S. guentheri* is not known, the reported size of this species is 20–96 mm SVL (Torres-Carvajal, 2000). Thus, the description of the postnatal development of the osteocranium of *S. guentheri* presented here might not include neonates as defined by Morafka et al. (2000). Except for two dry skulls (KU 147319, 147326), all specimens were cleared and double-stained following the methodology of Taylor and van Dyke (1985) and Wassersug (1976). The sex of each specimen was determined by dissection; specimens smaller than 44 mm SVL had undifferentiated gonads. Descriptions and illustrations were prepared with the aid of a stereo microscope equipped with a camera lucida.

The cranial osteology of the adult *Stenocercus guentheri* is based on the description of the largest cleared-and-double-stained specimen (KU 147412, 88 mm SVL, ♂). Because of visual distortion of the latter specimen, several structures were drawn from dry skulls when appropriate (i.e., no major differences with the largest specimen). Because no serial sections were made, nasal and orbitotemporal cartilages are not described. Allometric analyses also were excluded from this study. The nomenclature proposed by Oelrich (1956) is followed unless otherwise mentioned; I follow Cope (1892) and Underwood (1970) for the nomenclature of the hyoid

apparatus and scleral ossicles, respectively. To facilitate comparison with other studies of cranial osteology of lizards, synonyms and references are presented in parenthesis after each term, as appropriate. For those anglicized names that are widely accepted, synonyms representing the Latin name (e.g., articulare instead of articular) are not included. Mandibular and maxillary teeth were counted from the anterior to the posterior ends of each side, whereas premaxillary teeth were counted from the right end to the left end of the premaxilla.

All specimens were collected in Ecuador (Mulaló; 00°47'S, 78°34'W; 2990 m; Provincia Cotopaxi) and are deposited in the herpetological collection of The University of Kansas Natural History Museum and Biodiversity Research Center.

RESULTS

Cranial Osteology of Mature Individual

The amphikinetic skull of *Stenocercus guentheri* (Fig. 1) is elevated (skull height = 46% of skull length) and short (skull width = 71% of skull length). Marginal teeth are present on the maxillary arcade (i.e., premaxilla and maxillae) and palatal teeth are present on the pterygoids. The opisthotics-exoccipitals and parasphenoid-basisphenoid are indistinguishably fused and, therefore, are described as single units—otoccipitals and parabasisphenoid, respectively. The only elements that bear ornamentation are the frontal and the parietal, which form the margins of the pineal foramen. The mandible is dentigerous and V-shaped in dorsal and ventral profiles, and its greatest width is 87% of its total length (Fig. 2). Each mandibular ramus increases in height and width posteriorly. The rami meet anteriorly forming the mandibular symphysis, the cartilaginous part of which represents the fused anterior ends of Meckel's cartilages.

Dermatocranium

Premaxilla. This element forms the anteromedial margin of the snout and the medial margin of each fenestra exonarina (*apertura nasalis externa* Hallermann, 1994; *external naris* de Queiroz, 1987; Rieppel, 1981). The premaxilla (pm) bears a narrow posterodorsally oriented nasal process (*premaxillary spine* Cope 1892; Frost and Etheridge, 1989; *prenarial process, processus nasalis* Jollie, 1960), which extends between the nasals, and a broad anterior alveolar portion (Fig. 1A–C). The premaxilla articulates with the maxillae anterolaterally, nasals posteriorly, and nasal

cartilages in between. The short posterior end of the nasal process articulates with the anteromedial corners of the nasals. In ventral view (Fig. 1B), the premaxilla is separated from the vomers and bears a posteromedial incisive process (pip). This tongue-shaped process extends ventrally and is as wide as, but less than one half the length of, a premaxillary tooth. The incisive process (*spina premaxillaris*, *prevomerine process* Jollie, 1960) lacks posterolateral extensions and is not pierced by foramina. Along its posteroventral edge, the premaxilla bears a crest that extends from its posterolateral corners to the base of the incisive process. Unlike other lizards, such as most iguanines (de Queiroz, 1987), the ventral surface of the premaxilla of *Stenocercus guentheri* lacks posteroventral extensions at its articulation with the maxilla. Anteroventrally, the alveolar portion of the premaxilla bears six teeth (Fig. 1B).

Septomaxillae. The septomaxillae (sm) are dorsoventrally compressed and lie anteromedially within the nasal capsules, lateral to the nasal septum (Fig. 1C). They form the floor of the anteromedial portion of the nasal cavity and the roof of the cavum containing the vomeronasal organ. Ventrally, the cavum is supported by the vomers. The septomaxillae are anteroventrally oriented and articulate with the maxillae anterolaterally and the vomers ventrally.

Maxillae. The maxillae (m) occupy most of the anterolateral aspects of the skull between the orbits and the snout (Fig. 1A–C). In lateral aspect, each maxilla extends approximately half the length of the skull. In an anterior to posterior sequence, the dorsal margin of the maxilla articulates with the premaxilla, septomaxilla, nasal,

prefrontal, lacrimal, and jugal, respectively. The lateral surface of the preorbital facial process of the maxilla is concave and forms the ventral and posterodorsal rims of the fenestra exonarina. There are two (left) or three (right) anterior inferior alveolar foramina on the pars facialis of the maxilla. The anterodorsal margin of the facial process forms the posteromedial rim of the fenestra exonarina and overlaps the nasal anterolaterally. The posterior half of the pars facialis of the maxilla is flat; five labial foramina (lf) are present on the lateral surface. The orientation of the labial foramina shifts from posterior (most posterior foramen) to anterior (most anterior foramen). These foramina are arranged in a nearly straight line that parallels the ventrolateral margin of each maxilla and extends from the level of the third to the eleventh maxillary tooth. The part of the maxilla bearing the last seven teeth forms part of the floor of the orbit (Fig. 3), and is dorsally overlapped by the palatine anteriorly, the jugal laterally, and the ectopterygoid posteriorly. This portion also constitutes the anteromedial rim of the inferior orbital fenestra (iof; *foramen suborbitale* Wellborn, 1933; *inferior orbital foramen* Oelrich, 1956; *palatine fontanelle* Jollie, 1960) and forms the floor of the maxillopalatine foramen (*infraorbital canal* Jollie, 1960; *infraorbital foramen* de Queiroz, 1987; Kluge, 1962) anteriorly. The maxillopalatine foramen is less than half the size of the lacrimal foramen (Fig. 3). Each maxilla bears 18 medially recurved and laterally compressed teeth on a well-developed alveolar shelf (Fig. 1B, C). Each maxillary alveolar shelf forms the lateral margin of each fenestra exochoanalis (*choana* or *internal nostril* Bellairs and Kamal, 1981; *internal choana* Kluge, 1962) posteriorly and each fenestra

vomeronasalis externa (*foramen Jacobsoni* Wellborn, 1933) anteriorly. The latter two fenestrae are continuous (Fig. 1B)—i.e., palaeochoanate condition (Lakjer, 1927). The medial margin of the alveolar shelf bears a crest, which extends anteromedially to overlap the lateral portions of the posteroventral margin of the premaxilla.

Nasals. The nasals (n) articulate anteriorly with the nasal process of the premaxilla and posteriorly overlap the frontal, thereby forming most of the roof of the nasal capsules (Fig. 1A). The posterior halves of the nasals are ventrally concave and form a conspicuous depression of the skull table between the anterior margins of the orbits. Each nasal articulates with the premaxilla anterior to the internasal suture and is acuminate posteriorly. In an anterior to posterior sequence, the lateral margin of each nasal articulates with the maxilla, prefrontal, and frontal, respectively. The nasal-prefrontal articulation is interrupted posteriorly by the slender anterolateral processes of the frontal, which extend to a point anterior to the lacrimals; however, the nasals partially overlap these processes to meet the postfrontals. Anteriorly, the nasal forms the posterodorsal rim of the fenestra exonarina. The dorsal surface of each nasal bears two (right) or three (left) small foramina arranged on an oblique line parallel to the posterolateral margin of the bone. The posterolateral margin forms an angle of about 45° with the adjacent posteromedial margin.

Prefrontals. The prefrontals (pref) lie on the anterolateral aspects of the skull table and form the anterodorsal rims of the orbits and the posterior wall of the nasal capsules (Figs. 1, 3). Together with the frontal and palatines, the prefrontals border

the orbitonasal fenestra, which communicates between the nasal and orbital cavities. Each prefrontal articulates with the frontal and nasal dorsomedially, the maxilla anterodorsally and anterolaterally, and the lacrimal ventrolaterally. The anterior part of the articulation between the prefrontals and the anterolateral processes of the frontal is overlapped by the nasals (Fig. 1A). In posterior view, each prefrontal articulates with the lacrimal laterally and is separated ventrally from the palatine by connective tissue. The ventrolateral portion of the posterior surface of each prefrontal is notched (*incisura lacrimalis* Wellborn, 1933) and forms the medial margin of the lacrimal foramen (Fig. 3). Ventral to this foramen, the ventrolateral end of each prefrontal is separated from the lacrimal by connective tissue. Ventral to the prefrontal-frontal suture, each prefrontal bears a foramen (Fig. 1C), herein termed the prefrontal foramen (pff).

Lacrimals. The lacrimals (*lachrymals* or *lacrymals* Bellairs and Kamal, 1981; Camp, 1923; de Beer, 1937) are small and laterally compressed bones, each of which completes the anterior orbit between the prefrontal and jugal (Fig. 1A, C). Each lacrimal (l) articulates with the maxilla anteriorly, jugal ventrolaterally and posteromedially, and prefrontal dorsolaterally and medially. Ventromedially, the lacrimals are separated from the prefrontals by connective tissue. The medial aspect of each lacrimal is notched to form the lateral wall of the lacrimal foramen (Fig. 3).

Frontal. The frontal (f) lies between the orbits and forms most of the dorsal orbital margin (Fig. 1A, C). It is longer than wide and bears ornamentation that more or less corresponds to the pattern of the scales closely adhered to its dorsal surface.

Anteriorly, the frontal is W-shaped because of the presence of one anteromedial and two anterolateral processes, which are partially overlapped by the nasals. The anterolateral processes are thinner and longer than the anteromedial process and extend to a point anterior to the lacrimals. Each anterolateral process forms a conspicuous ridge that laterally borders the depression in the posterior portions of the nasals. The anterolateral processes articulate with the medial margin of the prefrontals; however, only the anterior and posterior portions of the anterolateral processes are dorsally exposed because of partial overlap by the nasals (Fig. 1A). The anteromedial process of the frontal articulates with the posteromedial margin of each nasal and meets the posterior end of the internasal suture. The transverse posterior margin of the frontal lies anterior to the posterior margin of the orbits and articulates with the anterior margin of the parietal. Medially, the posterior margin of the frontal is notched (Fig. 1A) to form more than half of the margin of the pineal foramen (pif). Posterolaterally, the frontal articulates with the anteromedial margin of the postfrontal.

Parietal. The parietal (pa) forms most of the posterior surface of the skull table and has dorsal ornamentation that slightly corresponds to the pattern of the scales closely adhered to the surface (Fig. 1A, C). Laterally, the parietal is medially concave and forms the medial rim of the supratemporal fossae (sf). The corpus of the parietal bears a pair of short anterolateral processes, as well as a pair of long supratemporal processes (*lateroventral processes* Rieppel, 1981; *parietal processes* Jollie, 1960; Wellborn, 1933). A prominent, ventrolateral descending process

connects the anterolateral and supratemporal processes and invests the lateral aspect of the taenia marginalis. The body of the parietal bears one medially concave longitudinal crest on each side. Each anterolateral process articulates with the posterior half of the medial margin of the postfrontal anteriorly and with the dorsal process of the postorbital laterally. The ventrally oriented supratemporal processes are laterally compressed and describe an angle of approximately 72°; the supratemporals overlap these processes ventrolaterally (Fig. 1A). The distal end of each supratemporal process articulates with the paraoccipital process (parp) of the otoccipital (Fig. 1D). The transverse anterior margin of the parietal articulates with the posterior margin of the frontal and encloses the pineal foramen medially. This foramen is mostly enclosed by a medial notch on the posterior margin of the frontal. Medially, the posteroventral surface of the parietal bears the parietal fossa, which receives the distal end of the cartilaginous processus ascendens of the supraoccipital.

Supratemporals. The supratemporals (sut) are laterally compressed, longitudinal bones with convex anterior margins (Fig. 1A). Each supratemporal (*squamosal* of many authors; *tabular* Broom, 1935; Camp, 1923; see Camp [1923], de Beer [1937], and Jollie [1960] for discussion on nomenclature) lies entirely on the posteroventral portion of the lateral surface of each supratemporal process of the parietal. The anterior end of each supratemporal extends halfway across the supratemporal fossa, whereas the posterior end articulates with the distal end of the paraoccipital process of the otoccipital, the cephalic condyle of the quadrate, the posterior end of squamosal, and the intercalary cartilage.

Postfrontals. The postfrontals (posf) are small, flat triangular bones that form part of the posterodorsal rims of the orbits (Fig. 1A, C). The medial margin of each postfrontal articulates with the anterolateral process of the parietal posteriorly and the posterior end of the lateral margin of the frontal anteriorly. The posterior margin of each postfrontal articulates with the anterior margin of the dorsal process of each postorbital.

Postorbitals. These triradiate bones (porb; *quadratojugals* Reese, 1923) lie on the posterolateral aspects of the skull posterior to the orbits (Fig. 1A, C). The anterior margin of each postorbital forms the posteroventral rim of the orbit, whereas the posterior margin forms the anterolateral rim of the supratemporal fossa. Each postorbital forms the anterior half of the supratemporal arch. The posterodorsally oriented ventral margin of the postorbital articulates anteriorly with the jugal and is separated posteriorly from the squamosal by a flexible ligament. The dorsal process of each postorbital extends dorsomedially and articulates with the posterior margin of the postfrontal anteriorly and with the anterolateral process of the parietal medially. Lateral to the articulation with the postfrontal, the dorsal process bears a short, wide, anterodorsally oriented knob (Fig. 1A, C), herein termed the anterodorsal postorbital process (apop).

Squamosals. The squamosals (sq; *paraquadrates* Gaupp, 1906; *supratemporals* of many authors; nomenclature discussed by Camp [1923], de Beer [1937], and Jollie [1960]) are long and slender, and form the posterolateral rims of the supratemporal fossae and the posterior halves of the supratemporal arches (Fig. 1A, C). The anterior

portion of the dorsal margin of each squamosal is separated from the posteroventral margin of the postorbital by a flexible ligament. Posteriorly, the squamosal is expanded and articulates dorsally with the posterior end of the supratemporal and ventrally with the cephalic condyle of the quadrate.

Jugals. Jugals (j) are broadly V-shaped and form the ventral rims of the orbits (Fig. 1A–C). Each jugal (*zygomaticum* Gaupp, 1906) is composed of two elongated processes that enclose and angle of 120°with the vertex lying halfway between the anterior and posterior ends of the skull (Fig. 1C). The anterior, or maxillary, process articulates ventrally with the posterodorsal portion of the maxilla (Fig. 3), posteromedially with the distal margin of the anterolateral process of the ectopterygoid, and anteriorly with the lacrimal. The dorsal half of the anterior margin of the posterior or temporal process articulates with the anterior portion of the ventral margin of the postorbital (Fig. 1C). Medially, the temporal process bears the maxillary foramen, which lies immediately anterior to the anteroventral end of the postorbital.

Vomers. Vomers (v; *prevomers* Camp, 1923; de Beer, 1937; Kluge, 1962; Williston, 1925) are the most anterior elements of the palate and form the medial border of each fenestra vomeronasalis externa (fv) anterolaterally and about 75% the length of the medial rim of each fenestra exochoanalis (fe) posterolaterally (Fig. 1B). The vomers articulate with each other along the anterior two thirds of their length and they are separated from the posteroventral margin of the premaxilla and premaxillary process of the maxilla by connective tissue. Each vomer has a small groove

anteriorly. The anterior half of each vomer bears a vomerine foramen (vf) and a lacrimal groove on its lateral aspect. There is a small notch anterior to the lacrimal groove that corresponds to the medial rim of the fenestra vomeronasalis externa. Posteriorly, the vomers are invested by the vomerine processes of the palatines. The posteromedial aspect of each vomer is dorsally concave.

Palatines. Palatines (pl) are medially separated by the anterior third of the pyriform space (pys; *pyriform recess* Oelrich, 1956). Each palatine bears three processes—viz., the vomerine anteromedially, the pterygoid posteriorly, and the maxillary anterolaterally (Fig. 1B). The vomerine process overlaps the corresponding vomer dorsally, thereby lying in the most dorsal aspect of the palate. Together with the anterior margin of the maxillary process, the lateral margin of the vomerine process forms the posteriorly concave rim of the fenestra exochoanalis. The wide quadrangular pterygoid process descends posteroventrally and forms the medial margin of the inferior orbital fenestra. This process overlaps the dorsal surface of the palatine process of the pterygoid posteriorly and bears a series of small foramina on its ventral surface. The short maxillary process forms the medial half of the anterior rim of the inferior orbital fenestra posteriorly. The maxillary process overlaps the dorsal surface of the maxilla at the level of the anterior end of the orbit forming the roof of the maxillopalatine foramen (Fig. 3).

Ectopterygoids. The ectopterygoids (ecp) form the posterolateral rims of the inferior orbital fenestrae (Fig. 1B). Each ectopterygoid (*transpalatine* de Beer, 1937; *transversum* Beddard, 1905; Gaupp, 1906; Wellborn, 1933) bears three

processes—viz., anterolateral, posterolateral, and medial processes. The anterolateral process overlaps the dorsal surface of the posterior portion of the maxilla bearing the last four maxillary teeth. Laterally, this process articulates with the posterior portion of the ventromedial margin of the maxillary process of the jugal. The anterior aspect of the short posterolateral process overlaps (with a thin layer of connective tissue in between) the anteroventral end of the temporal process of the jugal dorsally and the posterior end of the maxilla ventrally. The medial process bifurcates into dorsal and ventral branches, which firmly brace the anterior aspect of the transverse process of the pterygoid. The vertical ventral branch is shorter than the dorsal one.

Pterygoids. The pterygoids (pt) are the largest and most posterior elements of the palate and bear one tooth each (Fig. 1B–D). They form the posteromedial rim of each inferior orbital fenestra and, together with the parabasisphenoid, the rim of the posterior two thirds of the pyriform space. Anteriorly, each pterygoid bears two processes—the palatine medially and the transverse laterally. Each flat triangular palatine process forms the posterior quarter of the roof of the mouth and, dorsally, is overlapped by the pterygoid process of each palatine. Each transverse process extends dorsolaterally; distally, the transverse process is expanded and anteriorly embraced by the dorsal and ventral branches of the medial process of the ectopterygoid. Posteriorly, each pterygoid bears the long, laterally compressed quadrate process, which constitutes half the length of the bone. The quadrate process is medially concave, laterally convex, and extends posterolaterally to articulate with the ventral portion of the medial aspect of the quadrate (Fig. 1D). The anteromedial

aspect of each quadrate process bears the large pterygoid notch, which is fused with the overlying meniscus pterygoideus. The meniscus pterygoideus is partly ossified and receives the distal cartilaginous end of the basipterygoid process (bap) of the parabasisphenoid (Fig. 1B). The proximal end of the dorsal border of each quadrate process bears the columellar fossa (*fossa pterygoidei* Jollie, 1960), which receives the ventral end of each epipterygoid; posterior to the columellar fossa, the quadrate process bears a small elevation, the postcolumellar process (Fig. 4).

Scleral ossicles. The scleral ossicles (so) are thin plates of bone that lie in a circular depression (sulcus) that surrounds the cornea. The scleral ossicles maintain the concavity of the sulcus against the intraocular pressure (Underwood, 1970). There are 14 ossicles of similar size in each eye (Fig. 5). Each ossicle has a sigmoid flexure as it passes from the concavity of the sulcus to the convexity of the sclera (Underwood, 1970). Ossicles 1, 6, and 8 are plus (+) plates because they overlap both neighbors, whereas Ossicles 4, 7, and 10 are minus (–) plates because they are overlapped by both neighbors. This number and pattern of overlap of ossicles are fairly constant among iguanid lizards (de Queiroz, 1982; Gugg, 1939; Underwood, 1970) and, because all the ossicles contribute to the corneal margin of the ring, correspond with Pattern A (de Queiroz, 1982). Pattern A is widespread among iguanid lizards and, therefore, has been considered to be primitive for Iguania (de Queiroz, 1982).

Dentary. This anterolateral element is the largest of the mandibular bones and the only one that bears teeth (Fig. 2A–C). It is more than half the length of the lower

jaw laterally and bears 20 (21 on left ramus) teeth on a well-defined alveolar shelf. The dentary (*dentale* Gaupp, 1906; Versluys, 1936) invests the anterior half of Meckel's cartilage; however, the anterior end of the cartilage exits the dentary anterolingually through the anterior end of Meckel's canal, which lies ventral to the second tooth (Fig. 2B, C). Posteriorly, the dentary extends more than 50% the length from the apex of the coronoid to the anterior edge of the articular in lateral view. The posterior margin of the dentary articulates with several bones. Ventromedially, it is associated with the angular (Fig. 2C). Ventrolaterally and laterally, it articulates with the supra-angular and is overlapped dorsally by the labial process (lpc) of the coronoid (Fig. 2A). In lingual aspect, the dentary is bifurcate; the ventral splenial process and anteroventral portion of the dorsal coronoid process articulate with the splenial, whereas the posterior aspect of the dorsal coronoid process overlaps the anterior lingual process of the coronoid. Ventral to the third and fourth most posterior teeth, the dentary, splenial, and coronoid meet (Fig. 2B) to form the anterior inferior alveolar foramen (aiaf; *Meckelian foramen* Romer, 1956; Zalusky et al., 1980). The dorsolateral margin of the dentary, at its union with the coronoid, lies at the same level as the dorsal margin of the supra-angular. Laterally, the anterior half of the dentary bears five mental foramina (menf; *foramina dento-facialia* Versluys, 1936), which lie in a longitudinal series halfway between the ventral and dorsal margins (Fig. 2A).

Coronoid. The coronoid (*complementare* Gaupp, 1906) lies immediately behind the mandibular tooth row (Fig. 2A, B). It has a large dorsal process that extends

above the rest of the dorsal margin of the mandible; the height of the dorsal process is nearly as high as the maximum height of the dentary. Anteriorly, the base of the dorsal process is separated from the tooth row by connective tissue. Ventrolaterally, the coronoid bears a small labial process, which overlaps the dentary; the length of the labial process is less than one-fourth the height of the mandible at that point (Fig. 2A). Posterior to the labial process, the coronoid articulates ventrolaterally with the dorsal margin of the anterolateral process of the supra-angular. In medial aspect, the coronoid bears two processes (Fig. 2B). The anterior lingual process articulates with the dentary anteriorly, splenial ventrally, prearticular posteroventrally, and supra-angular posterodorsally. The posterior lingual process overlaps the anteromedial portions of the supra-angular dorsally and prearticular ventrally. The base of the lingual bifurcation of the coronoid is dorsally concave and articulates with the anterior end of the supra-angular.

Supra-angular. The supra-angular (*surangular* Cope, 1892; de Queiroz, 1987; Kingsley, 1905; Kluge, 1967; Rieppel, 1993; Romer, 1956; Zalusky et al., 1980) occupies the posterior half of the mandible and forms the dorsal portion of the lower jaw between coronoid and articular (Fig. 2A–C). In order to make a clear distinction between lateral and medial supra-angular foramina, I propose the names anterolateral (alsf) and posterolateral (plsf) supra-angular foramina instead of only anterior and posterior, respectively (Fig. 2A). In lateral aspect, the supra-angular is about one-third the length of the mandible and bears a narrow anterolateral process that extends between the coronoid dorsally and dentary ventrally. The dorsal margin of the distal

portion of this process articulates with the ventrolateral border of the coronoid posterior to the labial process. The ventral margin of the anterior process articulates with the posterodorsal border of the dentary. The anterolateral supra-angular foramen pierces the anterior process at about one-fourth the distance from the end of the process to its base. The ventrolateral border of the supra-angular articulates anteriorly with the lateral border of the angular and posteriorly with part of the lateral border of the prearticular, posterior to which the supra-angular and prearticular are indistinguishably fused (Fig. 2C). Laterally, the posterodorsal portion of the supra-angular bears two posterolateral supra-angular foramina (*foramen nervi auriculo-temporalis* Versluys, 1936), medial to which lie three additional small foramina (one on left ramus). Lingually, the anterior portion of supra-angular is overlapped by the coronoid; as a consequence, a small portion of the supra-angular is exposed between the lingual processes of the coronoid (Fig. 2B). The ventromedial and posteromedial margins of the supra-angular are fused with the prearticular. The articulation between the supra-angular and prearticular lies mainly along the lateral wall of what Romer (1956) referred as the adductor fossa (afs; *mandibular foramen* Oelrich, 1956; *mandibular fossa* Jollie, 1960; *Meckel's fossa* Wellborn, 1933), which is delineated by these two bones (Fig. 2B). On the posterolateral wall of the adductor fossa, the supra-angular bears a foramen, herein termed the posteromedial supra-angular foramen. On the anterolateral wall of the adductor fossa, the supra-angular bears a second foramen, which I designate as the anteromedial supra-angular foramen.

Prearticular. The prearticular (*articular* Cope, 1892; Kluge, 1962; Parker, 1880

1881; Rieppel, 1993; Wellborn, 1933; Zalusky et al., 1980; *dermarticulare* Kingsley, 1905; *goniale* Stimie, 1966; Versluys, 1936; *postoperculare* Gaupp, 1906) forms the posterior end of each mandibular ramus and lies mostly on the ventral and lingual aspects of the mandible (Fig. 2A–C). Posteriorly, the prearticular bears two triangular processes—the retroarticular process (rp) posteriorly and angular process (ap; *processus subarticularis* Siebenrock, 1895) medially. In dorsal view, the retroarticular process is defined by two rounded crests that converge posteriorly (Fig. 2B)—the tympanic crest (tc) laterally and the medial crest (mc) medially (de Queiroz, 1987). The medial crest bears the chorda tympani foramen (ctyf) at the medial side of its proximal end (Fig. 2B). A small foramen, herein designated the angular foramen, is present on the dorsal aspect of the angular process halfway between its posteromedial margin and the medial crest. Anterior to the angular and retroarticular processes, the dorsal aspect of the prearticular is fused with the overlying articular. The anteromedial portion of the prearticular is overlapped by the posterior lingual process of the coronoid and articulates with the supra-angular dorsally and the splenial ventrally. The anterormedial end of the prearticular also meets the posteroventral portion of the anterior lingual process of the coronoid. The dorsal margin of the remaining prearticular articulates with the ventromedial border of the supra-angular and forms the ventral wall of the adductor fossa (Fig 2B). The prearticular articulates anteroventrally with the angular and posteroventrally with the supra-angular; only the anterior portion of the prearticular-supra-angular suture is distinguishable (Fig. 2C).

Angular. As seen in ventral view (Fig. 2C), the angular comprises less than one-fourth the length of the mandible and lies along the ventral surface of each ramus. Its posterior margin is irregular and articulates laterally with the supra-angular and medially with the prearticular. Anteromedially, each angular bears a thin medial process that articulates laterally with the dentary, anteromedially with the splenial, and posteromedially with the prearticular. Ventromedially, each angular is pierced by a small, posteriorly directed posterior mylohyoid foramen (pmyf; *foramen nervi mylohyoid* Versluys, 1936) at the level of the anterior end of the adductor fossa (Fig. 2B, C).

Splenial. The small splenial (*operculare* Wellborn, 1933; *praeoperculare* Gaupp, 1906) is the only bone that is exposed solely on the medial aspect of the mandible (Fig. 2B). The anterior half of its dorsal margin articulates with the lingual coronoid process of the dentary anteriorly and the ventral border of the anterior lingual process of the coronoid posteriorly, whereas the posterior half articulates with the prearticular. The posterior half of the ventral border articulates with the lingual margin of the medial process of the angular. The anterior half of the ventral margin articulates with the dorsal border of the lingual splenial process of the dentary. The anterior end of the splenial forms the posterior rim of the anterior inferior alveolar foramen. The anterior portion of the splenial bears the anterior mylohyoid foramen (amyf), which is located at the same vertical level of the ventral rim of the adductor fossa (Fig. 2B). The anterior mylohyoid foramen is located posteroventral to the anterior inferior alveolar foramen.

Neurocranium

Basioccipital. The basioccipital (boc) lies between the otic capsules and forms the posterior floor of the braincase and the medial portion of the occipital condyle (oc; Fig. 1B, D). It articulates broadly with the parabasisphenoid anteriorly and is ventrally invested by the posterolateral processes of the parabasisphenoid anterolaterally. The basioccipital articulates with the inferior process of the prootic anterolaterally, and the cristae interfenestralis and tuberalis of the otoccipital posterolaterally. On each side, the basioccipital has a short ventrolateral process (*basioccipital process* Jollie, 1960) that projects ventrally as the spheno-occipital tubercle (sot; *basal tubera* Zalusky et al., 1980). Dorsally, the ventrolateral process bears a large occipital recess, which forms an antrum to the foramen rotundum (frot; Fig. 1D) with the otoccipital. The occipital recess described by Oelrich (1956) does not correspond to the recessus scalae tympani as argued by Rieppel (1985).

Supraoccipital. The anterodorsally oriented supraoccipital (soc) is a saddle-like bone that lies posteroventral to the parietal and forms the posterior roof of the braincase (Fig. 1A, D). The medial portion of its posteroventral margin forms the dorsal rim of the foramen magnum (fm; *foramen occipitale* Wellborn, 1933). The ventrolateral margin of the supraoccipital articulates with the dorsolateral margin of the alar process of the prootic anteriorly and the posterodorsal margin of the body of the otoccipital posteriorly. Its ventromedial margin articulates with the dorsomedial margin of the body of the otoccipital posteriorly and the posteromedial margin of the alar process of the prootic anteriorly. The anterodorsal margin of the supraoccipital is

separated from the parietal by a gap of connective tissue except for the medial cartilaginous processus ascendens (pasc), which extends anteriorly into the parietal fossa of the parietal (Fig. 1A, D). Posterior to this process, the dorsal surface of the supraoccipital bears a shallow depression on each side. A small process on each lateral end of the anterodorsal margin of the supraoccipital is fused to the posterior end of the taenia marginalis. The inner surfaces of the posteroventral and posterodorsal portions of the supraoccipital bear a deep, concave recess that is anteromedially oriented and that constitutes the anterior half of the auditory bulla; the posterior half is formed by the otoccipital. The auditory bulla is pierced on the posteroventral aspect of the supraoccipital by the endolymphatic foramen.

Parabasisphenoid. Except for its long anteromedial cultriform process (cup), the dermal parasphenoid is indistinguishably fused with the basisphenoid, which has both cartilaginous and membranous origins (Patterson, 1977; Rieppel, 1993). Therefore, these bones are described as a single parabasisphenoid (pbas; Fig. 1B, D). The parabasisphenoid (*sphenoid* de Beer, 1937; Gaupp, 1906; Kluge, 1962; Stimie, 1966) forms the anterior floor of the braincase. It articulates with the basioccipital posteriorly and the prootic dorsally. Its ventrolateral edges are formed by the cristae ventrolaterales and its anterodorsal edge is formed by the transverse crista sellaris. The parabasisphenoid bears three pairs of processes in addition to the cultriform process (*rostroparasphenoid* Jollie, 1960). Two thin, flat posterolateral processes overlap the basioccipital anterolaterally and extend to the anterodorsal aspect of its spheno-occipital tubercles. Between the proximal ends of these processes, the ventral

surface of the parabasisphenoid bears a recess. Anteriorly, two ventrolaterally oriented basipterygoid processes (*basitrabecular processes* Kluge, 1962; Säve-Söderbergh, 1947), which have expanded distal ends covered with articular cartilage, articulate with the partly ossified meniscus pterygoideus lying on the pterygoid notch of the quadrate processes of each pterygoid. Dorsal to each basipterygoid process, there is a short dorsolateral alar process (*clinoid process* Jollie, 1960), the distal end of which, together with the anterior end of the anteroventral process of the prootic, provides attachment for the pila antotica. Ventral to each alar process, the anterior surface of the parabasisphenoid bears the abducens canal. Laterally, the parabasisphenoid is pierced at the base of each posterolateral process by the entrance to the Vidian canal (*carotid* or *parabasal canal* Jollie, 1960), which exits through the ventrolateral portion of its anterior surface. Between these exits, the parabasisphenoid bears a short anteromedial process that overlaps the proximal end of the cultriform process (parasphenoid) and provides attachment for the bifurcate posterior end of the trabecula communis. This bifurcation corresponds to the posterior ends of the two trabeculae cranii, which fuse from front to back to form the trabecula communis in early developmental stages (tropibasic or tropitrabic skull [de Beer, 1937]). The thin, triangular cultriform process underlies the trabecula communis and extends anterodorsally to a point corresponding to the posterior limit of the maxillary arcade along the posterior half of the pyriform space.

Otoccipitals. Early in development, the exoccipital fuses with the opisthotic (*paroccipital* Williston, 1925) on each side of the braincase of most species of lizards

(de Beer, 1937; Gaupp, 1906; Oelrich, 1956). These elements are herein described as a single unit—otoccipital (otoc). The otoccipitals (*pleuro occipitale* Gaupp, 1906; Wellborn, 1933) form the posterolateral walls of the braincase and meet the prootics anterolaterally, supraoccipital dorsomedially, and basioccipital ventromedially (Fig. 1D). They form the lateral margins of the foramen magnum and lateral portions of the occipital condyle. Each otoccipital bears a lateral paraoccipital process (parp; *processus paroticus* Säve-Söderbergh, 1947; Versluys, 1898; Wellborn, 1933). The inner surface of the otoccipital has a deeply concave recess that forms the posterior half of the auditory bulla; the anterior half is formed by the supraoccipital. Two foramina pierce the posterior surface of each otoccipital between the most posterior portion of the auditory bulla (*ampulla canalis semicircularis frontalis* Wellborn, 1933; *internal semicircular canal* Cope, 1892) and the foramen magnum; these are the dorsal hypoglossal foramen (dhyf) ventrally, and the vagal foramen (vagf) dorsally (Fig. 1D). The paraoccipital processes extend posterolaterally and have expanded distal ends that are laterally compressed. A lateral extension of the auditory bulla forms a horizontal ridge that divides the posterior surface of each paraoccipital process into dorsal and ventral recesses. The distal end of each paraoccipital process is overlapped by the posterior end of the supratemporal anteriorly, the supratemporal process of the parietal dorsally, and the intercalary cartilage ventrally. The quadrate and squamosal also participate in this contact zone; however, they are separated from the paraoccipital process by the intercalary cartilage and the posterior end of the supratemporal, respectively (Fig. 6). Anterior to the paraoccipital process, each

otoccipital bears ventrally the posterior half of the posterior jugular recess; the anterior half of the jugular recess is formed by the prootic. The fenestra ovalis (*fenestra vestibuli* Gaupp, 1906; Jollie, 1960; Rieppel, 1992a), which lies mostly in the otoccipital and receives the footplate of the stapes, is located between the jugular recess and the foramen rotundum (*fenestra cochleae* Jollie, 1960; *fenestra rotunda* Säve-Söderbergh, 1947; Versluys, 1936). The anterior margin of the fenestra ovalis is formed by the medial margin of the posteroventral process of the prootic (Fig. 6). The medial wall of the jugular recess extends ventrally forming the crista interfenestralis, which separates the fenestra ovalis from the foramen rotundum. Posterior to this crista lies the anteroventrally oriented crista tuberalis, which bears laterally the ventral hypoglossal foramen on its proximal end. Together with the occipital recess of the basioccipital, the cristae interfenestralis and tuberalis form a large antrum to the foramen rotundum, which opens into the recessus scalae tympani. The medial and dorsal surfaces of the recessus scalae tympani are pierced by the foramen perilymphaticus (*foramen metotica, aqueductus cochleae* Jollie, 1960) and fenestra cochlea (*foramen perilymphaticum* Rao and Ramaswami, 1952; Rieppel, 1985), respectively. The foramen perilymphaticus opens into the cranial cavity through the anteroventral portion of the medial surface of each otoccipital. This part of the otoccipital also bears three posterodorsally directed hypoglossal foramina on the posteroventral portion, along with the vagal foramen (*jugular foramen* Jollie, 1960; Rieppel, 1985) on the posterodorsal portion. Dorsal to the foramen

perilymphaticus, each otoccipital forms the medial wall of the posterior auditory foramen; the lateral wall is formed by the prootic.

Prootics. The prootics (po; *otosphenoids* Siebenrock, 1895; Wellborn, 1933; *petrosals* Baur, 1889; Cope 1892) form the anterolateral walls of the braincase (Fig. 1C, D). Each bone bears three processes—viz., the alar (*superior anterior process* Jollie, 1960), anteroventral (*inferior process* Oelrich, 1956), and posterodorsal (*posterior process* Oelrich, 1956) processes. The short, anterodorsally oriented alar process articulates with the lateral margin of the supraoccipital posteriorly. The anterior margin of the alar process forms the crista alaris, ventral to which the prootic bears a lateral bulge that corresponds to the acoustic recess medially. This bulge forms the posterior portion of the trigeminal notch (*incisura prootica* Jollie, 1960; Säve-Söderbergh, 1947). The anteroventral process articulates with the parabasisphenoid anteriorly and the basioccipital ventrally. The pila antotica attaches to the anterior end of the suture between the prootic and the parabasisphenoid. The suture between the prootic and the basioccipital lies dorsal and parallel to the posterolateral process of the parabasisphenoid. The anteroventral process bears ventrally a large anteromedially oriented cavity, the anterior half of the anterior vena jugularis recess, which is pierced posteromedially by the facial foramen. The lateral margin of the anteroventral process forms the anterior half of the crista prootica (*crista otosphenoidea* Jollie, 1960; Wellborn, 1933), a longitudinal crest that runs from the posterodorsal to the anteroventral process forming the lateral wall of the anterior vena jugularis recess. The dorsal margin of the anteroventral process forms

the ventral portion of the trigeminal notch. The posterodorsal process of the prootic overlaps the anterior surface of the paraoccipital process of the otoccipital and its medial margin forms the anterior margin of the fenestra ovalis (Fig. 6). Medial to the crista prootica, the posterodorsal process forms both the posterior half of the anterior vena jugularis recess and the anterior half of the posterior vena jugularis recess. The vena jugularis recesses form the roof and medial wall of the tympanic cavity. Along its ventromedial margin, the prootic bears a crest that forms the short supratrigeminal process anteriorly. The deeply concave acoustic recess lies posteroventral to this process on the medial aspect of the prootic. The acoustic recess bears three foramina—viz., two anterior auditory foramina dorsally and the facial foramen ventrally. Posterior to this recess, the prootic forms the lateral wall of the posterior auditory foramen; the medial wall is formed by the otoccipital.

Orbitosphenoids. Anteromedial to the epipterygoids, the anteroposteriorly compressed orbitosphenoids (*laterosphenoids* Romer, 1956; Zalusky et al., 1980; *postoptics* Cope, 1892) lie along the posterior limit of the orbits (Figs. 1C, 7). The orbitosphenoids form the anterior aspect of the braincase and the lateral margins of the optic foramen (*optic fenestra* Zalusky et al., 1980). Each orbitosphenoid (o) is anterodorsally and posterolaterally oriented and continuous with the taenia parietalis media (*planum supraseptale* de Queiroz, 1987; Oelrich, 1956) anterodorsally, the pila accesoria and pila antotica posterodorsally, and the ventral portion of the pila metoptica (*taenia metoptica* Gaupp, 1906) ventrally. The dorsal portion of the pila metoptica is ossified as the orbitosphenoid.

Splanchnocranium

Quadrates. The quadrates (q), which are located at the posterolateral corners of the skull, articulate with and support the lower jaw (Figs. 1, 6). Ventrally, each quadrate bears a large condyle, which articulates with the medial and lateral portions of the glenoid fossa of the articular. A prominent crest extends posterodorsally from the transverse condyle to the dorsally convex cephalic condyle that lies on the posterodorsal end of each quadrate. The cephalic condyle articulates with the intercalary cartilage ventromedially, distal end of the supratemporal dorsomedially, and distal end of squamosal dorsolaterally. The intercalary cartilage separates the cephalic condyle from the paraoccipital process of the otoccipital (Fig. 6). The posterior crest divides each quadrate into a wide, anterolaterally concave lateral half with the tympanic crest along its lateral margin and a short medial half with the medial crest along its medial margin. The dorsolateral aspect of the lateral half is laterally notched (superior fossa) and attached to a small cartilaginous quadrate epiphysis that extends along the dorsolateral margin of each quadrate from the dorsal end of the tympanic crest to the cephalic condyle (Fig. 6). The anterior portion of the quadrate epiphysis is ossified as a thin plate of bone (qep; Fig. 1A). The medial half of the quadrate articulates with the quadrate process of the pterygoid ventromedially (Fig. 1D) and provides attachment for the processus internus of the extracolumella posterodorsally. The lateral half bears the anterior quadrate foramen on its anteroventral surface dorsal to the transverse condyle, whereas the medial half bears

the posterior quadrate foramen on its posteroventral surface dorsal to the articulation with the pterygoid.

Intercalary cartilages. A small intercalary cartilage (ic) separates the cephalic condyle from the paraoccipital process of the otoccipital (Figs. 1, 6) on each side. The intercalary cartilage (*processus paroticus* Bellairs and Kamal, 1981; *second supratemporal* Beddard, 1905) derives from the dorsal process of the columella auris early in development (Bellairs and Kamal, 1981; Rieppel, 1993) and has been reported as a separate element only for a few taxa, such as *Varanus* (Bahl, 1937; Varanidae) and *Uromastix* (Jollie, 1960; Agamidae).

Epipterygoids. The rod-shaped epipterygoids (epp) form a pair of vertical braces between the palate and the skull table (Fig. 1C). They are posterodorsally tilted and their dorsal halves laterally bowed, extending dorsally as far as the same vertical plane of the ventrolateral border of the parietal, from which they are separated by connective tissue. The dorsal end of each epipterygoid (*columella cranii* Wellborn, 1933; *columella, antipterygoid* Gaupp, 1906) is capped with partly ossified cartilage and the ventral end inserts into the columellar fossa of the quadrate process of the corresponding pterygoid (Fig. 4).

Middle ear. In addition to the tympanic membrane, the middle ear is composed of the bony stapes (sta) proximally and the cartilaginous extracolumella (ext) distally (Figs. 1, 6), which together form the columella auris (de Beer, 1937; Jollie, 1960; Stimie, 1966). Both the stapes and the extracolumella are about the same length. Each thin cylindrical stapes (*columella* Cope, 1892; Wever, 1978; *columella auris*

Bellairs and Kamal, 1981; Kluge, 1962; Oelrich, 1956; Rieppel, 1993; Romer, 1956) lies anteroventral to the paraoccipital process of the otoccipital and extends anteromedially between the extracolumella and the fenestra ovalis. The cartilaginous, expanded proximal end of the stapes forms an elongated footplate that attaches to the membrane covering the fenestra ovalis, the perimeter of which is only slightly larger than the perimeter of the footplate. The cartilaginous extracolumellae (*epistapedial cartilages* Cope, 1892; *extrastapes* Bellairs and Kamal, 1981; Rieppel, 1993) articulate with the distal ends of the stapes. *Stenocercus guentheri* has an iguanid type of middle ear (Wever, 1978)—i.e., the proximal portion of each extracolumella bears a laterally compressed processus internus (pint), which extends anteriorly to attach through its expanded anterior margin to the medial half of the quadrate. The distal end of each extracolumella is cruciform, bearing four elongate processes—the pars inferior (pinf) anteroventrally, the pars superior (psup) posterodorsally, the processus accesorius anterior anterodorsally (paca), and the processus accesorius posterior (pacp) posteroventrally (Fig. 6).

Meniscus pterygoideus. The meniscus pterygoideus (*cartilago articularis ossis pterygoidei* Gaupp, 1900) lies on each pterygoid notch forming part of the synovial joint between the basipterygoid processes and the pterygoids. Except for its dorsal border, each meniscus pterygoideus is ossified as a small ossicle inserted in the pterygoid notch.

Articular bone and Meckel's cartilage. The triradiate articular bone (*articular condyle* Parker, 1880; *prearticular* Oelrich, 1956) lies on the dorsal aspect of the

posterior portion of each mandibular ramus (Fig. 2A, B). The articular is located between the proximal portions of both the retroarticular and angular processes of the prearticular, with which it is fused. It is also fused anteriorly with the supra-angular. The articular has three processes—anterodorsal, posterolateral, and posteromedial. It also bears a pair of dorsal concavities, the medial and lateral portions of the glenoid fossa, which form the articular facet of the lower jaw. More than half of the articular is ossified. Meckel's cartilage is represented by three short, discrete segments; one lies in the adductor fossa, another at the level of the anterior inferior alveolar foramen, and the third one exits the anterior end of Meckel's canal (Fig. 2B). The latter segment meets its counterpart to form the cartilaginous portion of the mandibular symphysis.

Hyoid apparatus. The hyoid lies beneath the lower jaw and supports the tongue, throat muscles, and anterior portion of the trachea. It is composed of the basihyal (*body* Bellairs and Kamal, 1981; de Queiroz, 1987; Oelrich, 1956; Romer, 1956; *copula* Jollie, 1960; Romer, 1956; *corpus hyoideum* Romer, 1956), which forms the body of the hyoid apparatus, and three pairs of visceral arches (Fig. 8). Anteriorly, the basihyal bears a long and thin medial process, the glossohyal (*hypohyal* de Queiroz, 1987; Oelrich, 1956; *lingual process* Bellairs and Kamal, 1981; Jollie, 1960; Oelrich, 1956; Romer, 1956; *processus entoglossus* Gaupp, 1906). The first pair of visceral arches is attached to the anterolateral portions of the basihyal, and each arch is composed of an anterolaterally oriented short hypohyal (*basihyal* de Queiroz, 1987; *hyoid cornu, hyoid horn* Romer, 1956) and a long, posterolaterally oriented

ceratohyal (*cornu principale* Gaupp, 1906; *epihyal* Romer, 1956). The proximal end of each ceratohyal bears a medial dorsoventrally compressed process, herein termed the anteromedial ceratohyal process (acp). The second pair of visceral arches is attached to the posterolateral portions of the basihyal. Each arch is formed by the long, posterolaterally oriented first ceratobranchial (*Cornu Branchiale I*, Gaupp, 1906) anteriorly and the short first epibranchial (*cartilaginous dorsal process*, Romer, 1956) posteriorly. The third pair of visceral arches corresponds to the second pair of ceratobranchials (*Cornu Branchiale II*, Gaupp, 1906) and is continuous with the posterior portion of the basihyal. The posterior portions of all the visceral arches are dorsally oriented; a pair of short, posterodorsally oriented second epibranchials, which do not articulate with any structure, lies medial to the first ceratobranchials. The posterior end of each second epibranchial is expanded and lies medial to the anterior end. The cornua branchiale prima are the only completely ossified elements of the hyoid apparatus and the second epibranchials are the only unossified cartilaginous elements. All other elements are heavily calcified with only a thin cartilaginous sheath remaining.

Teeth

Marginal teeth. The premaxilla, maxillae, and dentaries bear 6, 18 (each), and 20 (21 on left ramus) marginal teeth, respectively (Figs. 1, 2). Premaxillary teeth are recurved posteriorly, laterally compressed, similar in size to the maxillary teeth, and lie on a well-developed alveolar shelf. Maxillary dentition is heterodont; Teeth 1–7 are conical or tricuspid with nearly inconspicuous lateral cusps, whereas Teeth 8–18

are tricuspid with the lateral cusps much smaller than the medial one. Maxillary tooth positions 5, 7, 10, 12, 14, and 17, and premaxillary tooth positions 2 and 4, bear replacement teeth. The position of the replacement teeth (i.e., lingual to the corresponding functional teeth) and the presence of resorption pits in the pulp cavity of some functional teeth indicate a typical iguanid pattern of tooth replacement (Edmund, 1960, 1969; Rieppel, 1978a).

Mandibular dentition is heterodont; teeth on the anterior third are conical or tricuspid with inconspicuous lateral cusps and teeth on the posterior two thirds are tricuspid with the lateral cusps smaller than the medial one. A replacement tooth (rt) is located on the medial side of each of Teeth 2, 4, 6, 8, 10, 13, 15, 16, 18, 19, and 20 on the right dentary (Fig. 2B) and Teeth 2, 4, 6, 9, 11, 14, 16, and 19 on the left dentary. The first and last two teeth are lower that the others, but because the portion of the shelf where the last two teeth are located is elevated, only the tips of Teeth 1 and 2 are lower than those of the other teeth.

Palatal teeth. Pterygoids are the only tooth bearing bones of the palate. Each pterygoid bears one, non-recurved, conical tooth on its ventral surface at the level of the posterior end of the inferior orbital fenestra (Fig. 1B).

Postembryonic Development

Dermatocranium

Of all of the dermal bones of the cranium of *Stenocercus guentheri*, the parietals undergo the greatest postnatal ontogenetic change (Fig. 9). At 30 mm SVL, only the

posterior halves of the parietals are fused, leaving a large, prominent frontoparietal fontanelle. The anterolateral corner of each parietal overlaps the posterolateral margin of the frontal; the anteromedial corner of each parietal is overlapped by the frontal. The parietals continue ossifying anteromedially and they are completely fused at 55 mm SVL (Fig. 9). Nevertheless, a small circular portion of the frontoparietal fontanelle remains unossified to form the pineal foramen. The proportional contribution of the parietal (i.e., fused parietals) and frontal (i.e., fused frontals) to the pineal foramen is variable and not related to size. In 58% of the specimens, the frontal forms only half of the pineal foramen, whereas in 42% of the specimens it forms more than half of this foramen. At a SVL of 30 mm, the portion of the parietals corresponding to the corpus of the adult single parietal is wider than long and the longitudinal lateral crests are nearly straight. Thus, the dorsal surface of the parietal corpus is about equal to the ventral surface. With increasing age and size, the anterolateral and posterolateral portions of the parietal grow faster than the corpus to reach the condition described for the largest specimen. Similar ontogenetic changes in the shape of the parietal roof have been described for other iguanid lizards, such as anolines (Etheridge, 1959), iguanines (de Queiroz, 1987), and leiocephalines (Etheridge, 1966; Pregill, 1992). Because of this change in shape, the anterolateral processes (as described for the largest specimen) cannot be distinguished in specimens smaller than 55 mm SVL. The distal ends of the supratemporal processes are short in small specimens, lying anterior to the posteroventral margin of the supraoccipital in specimens less than 60 mm SVL. The anterolateral processes

gradually overlap the posterolateral ends of the frontal until they articulate (through a thin layer of connective tissue) with 50% or more the length of the medial margin of the postfrontal in specimens larger than 74 mm SVL.

Other components of the skull table that vary ontogenetically are the frontal and postorbital. The anterolateral processes of the frontal are only slightly longer than the anteromedial process at 30 mm SVL; they become much longer than the anteromedial process with increasing age and size. The anteromedial process does not meet the posterior end of the internasal suture in specimens less than 39 mm SVL; thus, a gap of connective tissue (i.e., frontonasal fontanelle) remains. Regarding the postorbital, the anterodorsally-oriented knob of its dorsal process is nearly inconspicuous in specimens smaller than 35 mm SVL.

In a 30-mm individual, the ventrolateral margin of the coronoid is located dorsal to the dorsolateral margin of the dentary; these margins meet in a 35-mm specimen. In larger individuals, the coronoid develops a labial process that extends ventrally with age until it reaches the condition described for the largest specimen.

Neurocranium

Except for the medial portion of the basioccipital-parabasisphenoid articulation (i.e., basicranial fontanelle), all of the elements of the braincase are widely separated from one another by cartilage in a 30-mm lizard (Fig. 10). However, the bones of the braincase approach each other as ossification replaces the intervening cartilages in larger lizards. Thus, the cartilage separating the otoccipital from the basioccipital, and the prootic from the supraoccipital is almost completely ossified in a 68-mm

lizard. At 81 mm SVL, only the cartilage surrounding the parabasisphenoid and that between each prootic and each otoccipital remain unossified; all other bones are fused. The medial portion of the occipital condyle, which corresponds to the posterior end of the basioccipital, lies ventral to the lateral portions (formed by the otoccipitals) in a 30-mm individual (Fig. 10A). These medial and lateral portions are connected with cartilage that ossifies with age; in a 49-mm specimen, the basioccipital portion of the condyle lies at the same dorsal level as the otoccipital portions. The spheno-occipital tubercle and occipital recess of each basioccipital are poorly developed in specimens smaller than 35 mm SVL and 49 mm SVL, respectively. The cristae interfenestralis and tuberalis of the otoccipitals appear at 39 mm SVL, whereas the cristae prootica of the prootics, along with the vena jugularis recesses, can be distinguished at 44 mm SVL. The length of each paraoccipital process of the otoccipitals is smaller than the distance between the base of the process and the foramen magnum in specimens smaller than 60 mm SVL. In a 30-mm individual, the distal end of each paraoccipital process is embraced by a thick layer of cartilage, which is almost completely ossified in an 88-mm specimen. Unlike other lizards, such as large iguanines (de Queiroz, 1987), the orbitosphenoid does not vary ontogenetically.

Splanchnocranium

In specimens smaller than 44 mm, the medial halves of the quadrates are absent and the processus internus of each extracolumella is attached to the base of the cephalic condyle of each quadrate. The latter attachment moves medially with the

growth of the medial half of each quadrate. A small cartilaginous epiphysis overlies the dorsal end of the anterolateral aspect of each quadrate in the 30-mm individual. The medial aspect of this epiphysis ossifies with age, whereas the lateral aspect does not change (see description of largest specimen, Fig. 6). The ossified quadrate epiphysis has been erroneously described as the quadratojugal by several authors (Jollie, 1960). I was not able to determine the ossification pattern of the quadrate epiphysis by simple observation through the microscope because of visual distortion.

In a 30-mm-SVL individual, Meckel's cartilage is represented by a long longitudinal bar, a short posterodorsal bar, and a posterodorsal facet; the latter emerges through the posterodorsal portion of the prearticular to form the articular (Figs. 11, 12A). The flat longitudinal bar extends from the anterior end of the mandible, where it meets its counterpart through the mandibular symphysis, to the posterior end of the adductor fossa. At this level, it bears a posterodorsal bar that meets the anteroventral aspect of the articular. The longitudinal bar of Meckel's cartilage is exposed through the anteromedial groove of the dentary, the anterior inferior alveolar foramen, and the adductor fossa. In specimens smaller than 79 mm SVL, the posterodorsal bar is exposed lingually, because the prearticular does not articulate with the supra-angular at this level. In addition, the posterodorsal bar ossifies with age and it is completely ossified in a lizard 81 mm long. The degree to which Meckel's cartilage is exposed anteriorly varies with the position of the anterior end of Meckel's canal—it lies ventral to the fourth mandibular tooth in specimens less than 44 mm long, ventral to the third tooth in specimens between 44 and 79 mm

long, and ventral to the second tooth in larger specimens. However, Meckel's canal opens ventral to the fourth tooth and second tooth in two individuals 74 mm long (KU 147482) and 60 mm long (KU 147477), respectively. Whether the anterior ends of both Meckel's cartilages remain fused during postnatal life of lizards is unknown for most species (Bellairs and Kamal, 1981). This fusion was observed in all specimens of *S. guentheri* examined. A second center of ossification appears in the longitudinal bar at a level between the first and last mandibular teeth in individuals 39 mm long. Ossification progresses anteriorly and posteriorly with age and, together with a third center of ossification that appears at 44 mm SVL at the level of the coronoid, produces the condition described for the largest adult specimen. A small cartilage lies in the distal end of the retroarticular process of the prearticular in specimens smaller than 67 mm. This cartilage probably is a remnant of Meckel's cartilage that is isolated with the growth of the retroarticular process in earlier developmental stages.

Ossification of the articular was first evident in a 44-mm individual. The bone forms at the base of the anterodorsal process from a small, circular ossification center that is elongated through the posteromedial process in a 55-mm individual (Fig. 12B). In a lizard 65 mm long, the ossification center is expanded across the posterolateral process and another small ossification center has appeared in the anterodorsal process (Fig. 12C). Both ossification centers are present in larger specimens, except for KU 147369 (67 mm SVL) and KU 147482 (74 mm SVL), both of which lack the anterior center. These centers of ossification expand irregularly with age to reach the condition described for the largest adult specimen (Fig. 12D).

The posterior portion of the meniscus pterygoideus starts ossifying at 79 mm SVL, and at 88 mm SVL, only its dorsal border remains cartilaginous.

The only completely ossified elements of the hyoid apparatus in a 30-mm lizard are the cornua branchiale prima (first ceratobranchials) and the only fully cartilaginous elements are the second epibranchials, which do not ossify throughout ontogeny. All other elements show some ossification in the 30-mm individual; ossification progresses with age and size until all parts of the hyoid are heavily mineralized at 88 mm SVL except for the second epibranchials (Fig. 8). A small cartilage is attached to the proximal end of each first ceratobranchial at 30 mm SVL; this epiphysis is barely ossified in its center and ossifies gradually with age until no cartilage remains at 88 mm SVL. However, the fully ossified epiphysis at 88 mm SVL can be distinguished from the first ceratobranchial (Fig. 8).

Teeth

The numbers of teeth (mandibular, premaxillary, maxillary, and pterygoid) and replacement teeth of each specimen are presented in Table 2. There is obviously no correlation between the number of teeth and snout-vent length (Table 2); thus, the number of teeth does not vary ontogenetically as it does in other species of iguanid lizards (Montanucci, 1968; Ray, 1965). The number of teeth varies between 15–20 ($\bar{x}$ = 16.56 ± 1.42) on the right maxilla and 15–18 ($\bar{x}$ = 16.56 ± 1.1) on the left maxilla, 6–7 on the premaxilla (only one of 18 specimens with 7), 1–8 ($\bar{x}$ = 2.78 ± 1.77) on the right pterygoid and 1–7 ($\bar{x}$ = 2.44 ± 1.46) on the left pterygoid, and 18–23 on each dentary ($\bar{x}$ = 20.17 ± 1.15 right, 20.28 ± 1.13 left). Although the number of pterygoid

teeth varies between 1 and 8, only two specimens (44 mm and 55 mm SVL) have more than four pterygoid teeth (Table 2). These results are congruent with the intrapopulational variation in the number of pterygoid teeth reported by Cadle (1991) for two species of *Stenocercus* (*S. imitator* and *S. percultus*), in which the variation cannot be explained by ontogenetic or sexual factors. In all specimens, the premaxilla, maxillae, and dentaries bear replacement teeth, which do not vary ontogenetically in number. The position of replacement teeth on the maxillae and dentaries is similar for the left and right sides in most specimens (Table 2). The presence of replacement teeth in all the specimens suggests that tooth replacement starts before hatching and it does not cease with age (polyphyodonty), which seems to be the case for many species of lizards (Edmund, 1969; Lynch and Smith, 1964). Nonetheless, it has been demonstrated that the replacement rate in *Iguana iguana* decreases with age (Kline and Cullum, 1984, 1985).

DISCUSSION

Comparative Osteology and Systematics

Despite the application of osteocranial characters to elucidate the phylogenetic relationships among members of Iguania, only a few detailed descriptions of the osteocrania of iguanid lizards have been published (e.g., de Queiroz, 1987; Oelrich, 1956; Stimmie 1966), and none of them includes species of *Stenocercus*. Therefore, a comprehensive, comparative discussion of the osteological and systematic relevance of these data is not possible. However, I use herein information available in previous studies of lizard systematics (Cadle, 1991; Etheridge, 1966; Etheridge and de Queiroz, 1988; Frost, 1992; Frost and Etheridge 1989; Pregill, 1992) to compare cranial characters between *Stenocercus* and several closely related taxa. The following list includes only those osteological characters that differ between *Stenocercus guentheri* and related taxa, as revealed by the literature. These include: (1) nasal process of premaxilla overlapping nasal bones (nasal bones overlapping nasal process in *Leiocephalus*); (2) nasal process of premaxilla narrow (broad in *Plica, Strobilurus, Uracentron,* and *Uranoscodon*); (3) 6 premaxillary teeth (4 or 5 in *Uracentron, Strobilurus, Tapinurus, Uranoscodon, Plica plica,* and *Plica lumaria*); (4) no ontogenetic upward tilting of ventral margin of premaxilla (ontogenetic elevation of premaxilla in some species of Tropidurini, *Leiocephalus,* and *Stenocercus*); (5) prefrontal not in contact with margin of fenestra exonarina (in contact in *Tapinurus*); (6) supratemporal lying mostly on lateral surface of supratemporal process of parietal (supratemporal lying within groove in ventral

margin of supratemporal process of parietal in *Liolaemus* and *Ctenoblepharys*); (7) labial foramina of maxillae small (large in Tropidurini east of the Andes); (8) anterior maxillary teeth not enlarged in older adults (enlarged in some members of Tropidurini); (9) posterior maxillary teeth extending above edge of maxillae more than width of a tooth (teeth not extending far above edge of maxillae in *Tropidurus nanuzae*, *Uracentron flaviceps*, and *Plica*); (10) dentary extending posteriorly well beyond level of superior apex of coronoid (not extended in *Ctenoblepharys* and some members of Tropidurini); (11) coronoid process of dentary slightly overlapping anterior lingual process of coronoid (great overlap in Tropidurini except *Uranoscodon*); (12) dentary extending posteriorly more than 50% the length from apex of coronoid to anterior edge of articular (less than 50% extension in *Stenocercus* fide Frost [1992]); (13) alveolar shelf of dentary well defined (not well defined in Tropidurini); (14) coronoid labial process small (large in *Leiocephalus*, *Liolaemus*, and *Ctenoblepharys*); (15) Meckel's groove fused (unfused in *Ctenoblepharys*, *Liolaemus*, and some species of *Phymaturus*); (16) anterior surangular foramen not captured by contact of coronoid and dentary posterior to the foramen (captured in Tropidurini east of the Andes except *Uranoscodon* and *Tropidurus bogerti*); (17) posterior mylohyoid foramen pierces angular (not in Tropidurini east of the Andes except *Uranoscodon, Tropidurus spinulosus*, and *Uracentron*); (18) splenial not extending anteriorly more than one-sixth length of tooth row (variable in *Liolaemus* and extending more than one-sixth length of tooth row in *Ctenoblepharys*); (19) angular articulating with splenial on lingual surface of mandible (on ventral or labial

surfaces in *Phymaturus, Ctenoblepharys, Liolaemus, Leiocephalus, Tropidurus*, and *Uranoscodon*); (20) posterior mylohyoid foramen at the level of anterior end of adductor fossa (foramen located anterior [*Phymaturus, Ctenoblepharys, Liolaemus*] or posterior [*Uracentron, Tapinurus*] to this point; foramen located posterior to the anterior end of adductor fossa in *Stenocercus* fide Frost and Etheridge [1989]); (21) maxillopalatine foramen much smaller than lacrimal foramen (maxillopalatine foramen subequal in size to lacrimal foramen in *Plica, Uracentron*, and *Strobilurus*; lacrimal foramen not much larger than maxillopalatine foramen in *Stenocercus* fide Frost and Etheridge [1989]); and (22) pterygoid teeth present (absent in *Tropidurus bogerti, Plica umbra, Strobilurus torquatus, Tapinurus semitaeniatus, Uracentron azureum,* and some species of *Leiocephalus*; intraspecific variation in some species of *Stenocercus*).

Cadle (1991) summarized the observations on the presence/absence of pterygoid teeth reported in the literature (Boulenger, 1885, 1899, 1900, 1901, 1911; Frost, 1988; Parker, 1934; Griffin, 1917; Noble, 1924). He noted that nearly all species that had been recorded originally as lacking pterygoid teeth were subsequently reported to have them. This suggests that the presence/absence of pterygoid teeth varies intraspecifically in *Stenocercus*, and only a comprehensive study using appropriate sample sizes will elucidate the distribution of this character in this genus. My data indicate that pterygoid teeth are invariably present in a single population of *Stenocercus guentheri* and that their variation in number is unrelated to sex or age. The number of marginal teeth (i.e., premaxillary, maxillary, mandibular) does not

vary significantly within the population. Finally, I did not find any osteological differences between sexes other than adult males having wider skulls than females.

Functional Morphology and Kinesis

Traditionally, the cranial bones of lizards are grouped into three units: dermal skull roof, palate, and braincase. This approach is based on the function of the homologous bones in primitive tetrapods, such as the labyrinthodont *Palaeogyrinus* or the seymouriamorphans *Seymouria* and *Kotlassia* (Romer, 1956). However, the traditional classification is inconsistent with the actual function of some of the elements of the skull in lizards. This problem is reflected in the confusing way in which some elements have been classified. For example, the quadrate has been considered an element of both the palate (e.g., Romer, 1956; Hikida, 1978) and the skull roof (e.g., de Queiroz, 1987). There are several bones in the skull of *Stenocercus guentheri* (and most lizards) that have different functions than do their homologues in primitive tetrapods. The squamosal, postorbital, and jugal do not form part of the solid shield of bone protecting the top and sides of the head known as dermal skull roof. Instead, these three bones, together with the quadrate, epipterygoid, ectopterygoid, and pterygoid, are mainly components of the suspensorium. They also contribute significantly to the kinesis of the skull by constituting a site of mobility in the lateral postorbital region, which is characteristic of iguanids (Arnold, 1998). Because the squamosal and postorbital (temporal arch) are not firmly articulated with any other bone (Fig. 1), the temporal region of the skull has considerable flexibility. The postorbital can rotate around its articulation

with the parietal and, at the same time, its posterior process can lift away from the squamosal (Arnold, 1998). On the other hand, the anterior half of the jugal is firmly attached to, and supports the maxillary arcade. The posterodorsal portion of the premaxilla and the dorsal aspect of the maxillae that overlap the nasals are other primary sites of support of the maxillary arcade. The supratemporal is another element that has lost its function of roofing the skull; it provides a point of attachment for the quadrate, along with the parietal, squamosal, and otoccipital. Thus, the function of a solid shield of bones protecting the head dorsally is limited to the nasals, prefrontals, frontal, postfrontals (although they are very small), and parietal (Fig. 1). In addition, the sides of the head are fenestrate; the rostrum is the only region that is completely covered with bones (maxillae, prefrontals, and lacrimals). The palates of lizards also differ from those of primitive tetrapods. As mentioned above, the ectopterygoids are components of the suspensorium rather than elements of the palate, which is the case in primitive tetrapods. They are attached to the posterior ends of the maxillary arcade and provide support for the highly movable pterygoids by bracing them firmly. Similar to the skulls of most other lizards (Frazetta, 1962; Rieppel, 1978b, c), the skull of *Stenocercus guentheri* is amphikinetic and the quadrate can rotate around its dorsal suspension (streptostyly). The skull of this species has all the joints described by Bellairs and Kamal (1981) that are involved in mesokinesis and metakinesis (Versluys, 1912). Streptostyly is greatly facilitated by the presence of the intercalary cartilage, which provides more flexibility to the complex dorsal suspension of the quadrate (Fig. 6). Apparently, mesokinesis in

young individuals of *S. guentheri* is greatly enhanced by the incomplete frontoparietal suture and the high flexibility provided by the frontoparietal fontanelle.

Postembryonic Ossification of the Skull Roof in Lizards

Although information on the postembryonic development of the cranium in lizards is scarce, some differences in patterns of ossification of the skull roof can be described. Herein, I comment on the postembryonic ossification of the parietals in *Stenocercus guentheri* and eight other taxa—viz., *Acontias meleagris* (Scincidae), *Anniella* (Anniellidae), *Calotes versicolor* (Agamidae), *Cyrtodactylus pubisulcus* (Gekkonidae), *Eumeces latiscutatus* (Scincidae), *Lacerta vivipara, Podarcis muralis,* and *P. sicula* (Lacertidae). On one hand, from the descriptions of late embryos of the small fossorial lizards *Acontias* and *Anniella* (Brock, 1941 and Bellairs, 1950, respectively), it can be deduced that neonates of these species have fused parietals. Rieppel (1984) proposed that one reason for this pattern might be that the dermatocranium and neurocranium serve as a suspensorium for the jaws and their muscles in hatchlings of these fossorial lizards. On the other hand, neonates of most lizards have incomplete skull roofs (i.e., unfused frontals and/or parietals). This condition has been reported for many iguanids (Hallermann, 1992). The degree to which the frontals and parietals are fused in neonates and, consequently, the size of the frontoparietal fontanelles, vary interspecifically. For example, similar to *Stenocercus guentheri*, neonates of *Podarcis muralis*, *P. sicula*, *Lacerta vivipara*, and *Calotes versicolor* have large frontoparietal fontanelles (Rieppel, 1984, 1987, 1992a, and Ramaswami, 1946, respectively), whereas in hatchlings of *Cyrtodactylus*

pubisulcus and *Eumeces latiscutatus* the frontoparietal fontanelles are almost closed (Rieppel, 1992b and Hikida, 1978, respectively). In addition, the pattern of postembryonic ossification of the parietals also varies among these species. Even though a neonate of *Stenocercus guentheri* was not included in the present work, it can be deduced from the smallest specimen examined (KU 147347, 30 mm SVL) that the parietals of the hatchling are widely separated and ossify in two directions (i.e., posterior-anterior and lateral-medial, Fig. 9). This pattern has been reported for species like *Lacerta vivipara* (Rieppel, 1992a) and *Eumeces latiscutatus* (Hikida, 1978), although the parietals in newborn hatchlings of the latter species are almost completely fused. However, *S. guentheri* differs from *L. vivipara* and *E. latiscutatus* in that the parietals ossify without leaving a narrow longitudinal parietal fontanelle that extends from the frontoparietal suture to the position of the pineal foramen (i.e., halfway between the anterior and posterior margins of the parietal) as is the case in *L. vivipara* and *E. latiscutatus*. This difference is clearly related to the position of the pineal foramen, which is located in the frontoparietal suture in *S. guentheri*. The gekkonid *Cyrtodactylus pubisulcus* exhibits a different pattern of postembryonic development of the parietals. This species is unique in having a cruciform fontanelle formed by a longitudinal opening between the parietals and a short, transverse slit that intersects this longitudinal opening posterior to the point halfway between the anterior and posterior margins of the parietals (Rieppel, 1992b); the parietals ossify in a lateromedial direction until they fuse in later developmental stages.

The morphology and postembryonic development of the osteocranium of *Stenocercus guentheri* was described in this study. Although the results presented here contribute to our knowledge of the cranial morphology in lizards, we still lack information to gain a better understanding of the patterns of morphological and developmental diversity of the cranium (and postcranium) in lizards. Even general information of all extant saurian families is unavailable; this indicates clearly that basic research on the osteology of lizards is needed. An additional purpose of this study was to identify new cranial osteological characters that could be used for phylogenetic analyses of *Stenocercus*. The utility of these will only become apparent once the cranial osteology of other species of *Stenocercus* (and other iguanid lizards) has been investigated and the characters examined in a phylogenetic context.

LITERATURE CITED

Andrews RM. 1982. Patterns of growth in reptiles. In: Gans C, Pough H, editors. Biology of the reptilia. Vol.13. Physiology D. London and New York: Academic Press. p 273–320.

Arnold EN. 1998. Cranial kinesis in lizards. Variations, uses, and origins. Evol Biol 30:323–357.

Bahl KN. 1937. Skull of *Varanus monitor* (Linn.). Rec Indian Mus 39:133–174.

Baur G. 1889. On the morphology of the vertebrate skull. J Morphol Physiol 3(3):467–474.

Beddard FE. 1905. Some notes on the cranial osteology of the mastigure lizard, *Uromastix*. Proc Zool Soc Lond 1905:2–9.

Bellairs Ad'A. 1950. Observations on the cranial anatomy of *Anniella*, and a comparison with that of other burrowing lizards. Proc Zool Soc Lond 119:887–904.

Bellairs Ad'A, Kamal AM. 1981. The chondrocranium and the development of the skull in recent reptiles. In: Gans C, Parsons T, editors. Biology of the reptilia. Vol.11. Morphology F. London and New York: Academic Press. p 1–263.

Boulenger GA. 1885. Catalogue of the lizards in the British Museum (Natural History). Vol. 2. London: Taylor and Francis.

Boulenger GA. 1899. Descriptions of new reptiles and batrachians collected by Mr. P. O. Simons in the Andes of Ecuador. Ann Mag Nat Hist Lond 4(24):454–457.

Boulenger GA. 1900. Descriptions of new batrachians and reptiles collected by Mr. P. O. Simons in Peru. Ann Mag Nat Hist Lond 6(32):181–186.

Boulenger GA. 1901. Further descriptions of new reptiles collected by Mr. P. O. Simons in Peru and Bolivia. Ann Mag Nat Hist Lond 7(42):546–549.

Boulenger GA. 1911. Description of new reptiles from the Andes of South America, preserved in the British Museum. Ann Mag Nat Hist Lond 12:19–25.

Brock GT. 1932. Some developmental stages in the skulls of the geckos, *Lygodactylus capensis* and *Pachydactylus maculosa*, and their bearing on certain important problems in lacertilian craniology. S Afr J Sci 29:508–532.

Brock GT. 1940. The skull of the chamaeleon, *Lophosaura ventralis* (Gray); some developmental stages. Proc Zool Soc Lond 110(B):219–241.

Brock GT. 1941. The skull of *Acontias meleagris*, with a study of the affinities between lizards and snakes. Zool J Linn Soc 41:71–88.

Broom R. 1935. On the structure of the temporal region in lizard skulls. Ann Transvaal Mus 18:13–22.

Cadle JE. 1991. Systematics of lizards of the genus *Stenocercus* (Iguania: Tropiduridae) from northern Perú: new species and comments on relationships and distribution patterns. Proc Acad Nat Sci Philadelphia 143:1–96.

Camp CL. 1923. Classification of the lizards. Bull Am Mus Nat Hist 48:289–481.

Cope ED. 1892. The osteology of the lacertilia. Proc Am Philos Soc 13:185–221.

de Beer GR. 1930. The early development of the chondrocranium of the lizard. Q J Micr Sci 73:707–739.

de Beer GR. 1937. The development of the vertebrate skull. London: Oxford University Press. 515 p.

de Queiroz K. 1982. The scleral ossicles of sceloporine iguanids: a reexamination with comments on their phylogenetic significance. Herpetologica 38:302–311.

de Queiroz K. 1987. Phylogenetic systematics of iguanine lizards: a comparative osteological study. Univ Ca Publ Zool 118:1–203.

Edmund AG. 1960. Tooth replacement phenomena in the lower vertebrates. R Ontario Mus Life Sci Div Contr 52:1–190.

Edmund AG. 1969. Dentition. In: Gans C, Bellaris A, Parsons T, editors. Biology of the reptilia. Vol.1. Morphology A. London and New York: Academic Press. p 117–200.

Etheridge R. 1959. The relationships of the anoles (Reptilia: Sauria: Iguanidae). An interpretation based on skeletal morphology. PhD Dissertation. Ann Arbor: University of Michigan.

Etheridge R. 1966. The systematic relationships of West Indian and South American lizards referred to the iguanid genus *Leiocephalus*. Copeia 1:79–91.

Etheridge R, de Queiroz K. 1988. A phylogeny of iguanidae. In: Estes R, Pregill G, editors. Phylogenetic relationships of the lizard families: essays commemorating Charles L. Camp. Stanford: Stanford University Press. p 283–367.

Frazetta TH. 1962. A functional consideration of cranial kinesis in lizards. J Morphol 111:287–320.

Fritts TH. 1974. A multivariate and evolutionary analysis of the andean iguanid lizards of the genus *Stenocercus*. San Diego Soc Nat Hist Mem 7:1–89.

Frost DR. 1988. A phylogenetic analysis of the *Tropidurus* group of iguanian lizards, with comments on the relationships within the Iguania (Squamata). PhD Dissertation. Lawrence: University of Kansas.

Frost DR. 1992. Phylogenetic analysis and taxonomy of the *Tropidurus* group of lizards (Iguania: Tropiduridae). Am Mus Novit 3033:1–68.

Frost DR, Etheridge R. 1989. A phylogenetic analysis and taxonomy of iguanian lizards (Reptilia: Squamata). Univ Kansas Misc Publ Mus Nat Hist 81:1–65.

Gaupp E. 1891. Die Columella der kionokranen Saurier. Anat Anz 6:107–117.

Gaupp E. 1900. Das Chondrocranium von *Lacerta agilis*. Anat Hefte 15(3):435–594.

Gaupp E. 1906. Die Entwickelung des Kopfskelettes. In: Hertwig O, editor. Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere. Vol. 3. Part 2. Jena: Verlag von Gustav Fischer. p 573–873.

Griffin LE. 1917. A list of the South American lizards of the Carnegie Museum, with descriptions of four new species. Ann Carnegie Mus 11:304–320.

Gugg W. 1939. Der Skleralring der plagiotremen Reptilien. Zool Jb Anat 65:339–416.

Hallermann J. 1992. Morphological significance of the orbitotemporal region in amphikinetic skulls of juvenile iguanians (Squamata). Zool Jb Anat 122:203–206.

Hallermann J. 1994. Zur Morphologie der Ethmoidalregion der Iguania (Squamata)–Eine vergleichend-anatomische Untersuchung. Bonner Zool Monogr 35:1–133.

Hikida T. 1978. Postembryonic development of the skull of the Japanese skink, *Eumeces latiscutatus* (Scincidae). Japanese J Herpetol 7(3):56–72.

Jollie MT. 1960. The head skeleton of the lizard. Acta Zool 41:1–64.

Kingsley JS. 1905. The bones of the reptilian lower jaw. Am Nat 39(458):59–64.

Kline LW, Cullum DR. 1984. A long term study of the tooth replacement phenomenon in the young green iguana, *Iguana iguana*. J Herpetol 18(2):176–185.

Kline LW, Cullum DR. 1985. Tooth replacement and growth in the young green iguana *Iguana iguana*. J Morphol 186:265–269.

Kluge AG. 1962. Comparative osteology of the eublepharid lizard genus *Coleonyx* Gray. J Morphol 110:299–332.

Kluge AG. 1967. Higher taxonomic categories of gekkonid lizards and their evolution. Bull Am Mus Nat Hist 135(1):1–59.

Lakjer T. 1927. Studien über die Gaumenregion bei Sauriern im Vergleich mit Anamniern und primitiven Sauropsiden. Zool Jb Anat 49:57–356.

Lynch JD, Smith HM. 1964. Tooth replacement in a senile lizard, *Anolis equestris* Merrem. Herpetologica 20(1):70–71.

Macey JR, Larson A, Ananjeva NB, Papenfuss TJ. 1997. Evolutionary shifts in three major structural features of the mitochondrial genome among iguanian lizards. J Mol Evol 44:660–674.

Montanucci RR. 1968. Comparative dentition in four iguanid lizards. Herpetologica 24(4):305–315.

Morafka DJ, Spangenberg EK, Lance VA. 2000. Neonatology of reptiles. Herpetol Monogr 14:353–370.

Noble GK. 1924. New lizards from northwestern Peru. Occ Papers Boston Soc Nat Hist 5:107–113.

Oelrich TM. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Univ Michigan Misc Publ Mus Zool, 94:1–122.

Parker HW. 1934. Reptiles and amphibians from southern Ecuador. Ann Mag Nat Hist Lond 14:264–273.

Parker WK. 1880. On the structure and development of the skull in the lacertilia. Part I.–On the skull of the common lizards (*Lacerta agilis*, *L. viridis*, and *Zootoca vivipara*) Philos Trans R Soc Lond (Biol) 170:595–640.

Parker WK. 1881. On the structure of the skull in the chameleons. Trans Zool Soc Lond 11(4):77–105.

Patterson C. 1977. Cartilage bones, dermal bones and membrane bones, or the exoskeleton versus the endoskeleton. In: Andrews SM, Miles RS, Walker AD, editors. Problems in vertebrate evolution. London and New York: Academic Press. p 77–121.

Pearson HS. 1921. The skull and some related structures of a late embryo of *Lygosoma*. J Anat 56:20–43.

Pregill GK. 1992. Systematics of the West Indian lizard genus *Leiocephalus* (Squamata: Iguania: Tropiduridae). Univ Kansas Misc Publ Mus Nat Hist 84:1–69

Ramaswami LS. 1946. The chondrocranium of *Calotes versicolor* (Daud.) with a description of the osteocranium of a just-hatched young. Q J Micr Sci 87:237–297.

Rao MKM, Ramaswami LS. 1952. The fully formed chondrocranium of *Mabuya* with an account of the adult osteocranium. Acta Zool Stockh 33:209–275.

Ray CE. 1965. Variation in the number of marginal tooth positions in three species of iguanid lizards. Breviora 236:1–15.

Reese AM. 1923. The osteology of the tegu, *Tupinambis nigropunctatus*. J Morphol 38:1–17.

Rice EL. 1920. The development of the skull in the skink, *Eumeces quinquelineatus* L. I. The chondrocranium. J Morphol 34:119–243.

Rieppel O. 1978a. Tooth replacement in anguinomorph lizards. Zoomorphol 91:77–90.

Rieppel O. 1978b. The phylogeny of cranial kinesis in lower vertebrates, with special reference to the lacertilia. N Jb Geol Paläont 156:353–370.

Rieppel O. 1978c. Streptostyly and muscle function in lizards. Experientia 34:776–777.

Rieppel O. 1981. The skull and jaw adductor musculature in chamaleons. Rev Suisse Zool 88(2):433–445.

Rieppel O. 1984. The upper temporal arcade of lizards: an ontogenetic problem. Rev Suisse Zool 91(2):475:482.

Rieppel O. 1985. The recessus scalae tympani and its bearing on the classification of reptiles. J Herpetol 19(3):373–384.

Rieppel O. 1987. The development of the trigeminal jaw adductor musculature and associated skull elements in the lizard *Podarcis sicula*. J Zool Lond 212:131–150.

Rieppel O. 1992a. Studies on skeleton formation in reptiles. III. Patterns of ossification in the skeleton of *Lacerta vivipara* Jacquin (Reptilia, Squamata). Fieldiana Zool 68:1–25.

Rieppel O. 1992b. Studies on skeleton formation in reptiles. I. The postembryonic development of the skeleton in *Cyrtodactylus pubisulcus* (Reptilia: Gekkonidae). J Zool Lond 227:87–100.

Rieppel O. 1993. Patterns of diversity in the reptilian skull. In: Hanken J, Hall BK, editors. The skull. Vol. 2. Patterns of structural and systematic diversity. Chicago: University of Chicago Press. p 344–390.

Romer AS. 1956. Osteology of the reptiles. Chicago: University of Chicago Press. 772 p.

Säve-Söderbergh G. 1947. Notes on the brain-case in *Sphenodon* and certain lacertilia. Zool Bidrag Fran Uppsala 25:489–516.

Schulte JA, Macey JR, Larson A, Papenfuss TJ. 1998. Molecular tests of phylogenetic taxonomies: a general procedure and example using four subfamilies of the lizard family iguanidae. Mol Phylo Evol 10(3):367–376.

Sewertzoff AN. 1900. Zur Entwicklungsgeschichte von *Ascabalotes fascicularis*. Anat Anz 18:33–40.

Siebenrock F. 1892. Zur Kenntnis des Kopfskelettes des Scincoiden, Anguiden und Gerrhosuriden. Ann K K Naturhist Hofmus Wien 7:163–196.

Siebenrock F. 1893a. Das Skelett von *Uroplates fimbriatus* Schneid. Ann K K Naturhist Hofmus Wien 8:517–536.

Siebenrock F. 1893b. Das Skelett von *Brookesia superciliaris* Kuhl. Sitz Akad Wiss Wien 102:73–118.

Siebenrock F. 1894. Skelett der *Lacerta simonyi* Steind. und der Lacertidenfamilie überhaupt. Sitz Akad Wiss Wien 103:205–292.

Siebenrock F. 1895. Das Skelett der Agamidae. Sitz Akad Wiss Wien. 104:1089–1196.

Stimie M. 1966. The cranial anatomy of the iguanid *Anolis carolinensis* (Cuvier). Ann Univ Stellenbosch 41(3):243–268.

Taylor W, van Dyke G. 1985. Revised procedure for staining and clearing small fishes and other vertebrates for bone and cartilage study. Cybium 9:107–119.

Torres-Carvajal O. 2000. Ecuadorian lizards of the genus *Stenocercus* (Squamata: Tropiduridae). Sci Pap Mus Nat Hist Univ Kansas 15:1–38.

Underwood G. 1970. The eye. In: Gans C, Parsons T, editors. Biology of the reptilia. Vol 2. Morphology B. London and New York: Academic Press. p 1–97.

Versluys J. 1898. Die mittlere und äussere Ohrsphäre der Lacertilia und Rhynchocephalia. Zool Jb Anat 12:161–406.

Versluys J. 1912. Das Streptostylie-Problem und die Bewegungen im Schädel der Sauropsiden. Zool Jb Anat 15:545–716.

Versluys J. 1936. Kranium und Visceralskelett der Sauropsiden. In: Bolk L, Göppert E, Kallius E, Lubosch W, editors. Handbuch der vergleichenden Anatomie der Wirbeltiere. Vol 4. Berlin andVienna: Urban & Schwarzenberg. p 699–808.

Wassersug R. 1976. A procedure for differential staining of cartilage and bone in whole formalin-fixed vertebrates. Stain Technol 51:131–134.

Wellborn V. 1933. Vergleichende osteologische Untersuchungen an Geckoniden, Eublephariden und Uroplatiden. Sber Ges Naturf Fre Berlin 1933:126–199.

Wever EG. 1978. The reptile ear. Princeton University Press: New Jersey. 1024 p.

Williston SW. 1925. The osteology of the reptiles. Cambridge: Harvard University Press. 300 p.

Zalusky SB, Gaudin AJ, Swanson JR. 1980. A comparative study of cranial osteology in the North American sand lizards, genus *Uma* (Reptilia: Iguanidae). Copeia 2:296–310.

TABLES

Table 1. Specimens of *Stenocercus guentheri* examined.

Specimen no.	SVL (mm)	Skull length (mm)	Sex
KU 147347	30	9.6	—
KU 147525	32	9.8	—
KU 147520	35	11.1	—
KU 147346	39	11.2	—
KU 147519	44	12.7	female
KU 147534	49	13.4	male
KU 147445	55	14.6	female
KU 147477	60	15.1	female
KU 147409	65	17.1	male
KU 147326	66	15.8	female
KU 147369	67	16.6	female
KU 147382	68	16.6	female
KU 147487	70	17.3	male
KU 147482	74	18.0	male
KU 147319	78.5	19.8	male
KU 147421	79	18.8	male
KU 147388	81	18.5	male
KU 147412	88	20.3	male

Table 2. Number of teeth of the specimens of *Stenocercus guentheri* examined. Replacement teeth are indicated in parentheses. L, left; R, right.

SVL (mm)	Sex	Premaxillary Teeth	Mandibular Teeth		Maxillary Teeth		Palatal Teeth	
			L	R	L	R	L	R
30	—	6 (4)	20 (11)	20 (13)	15 (9)	15 (9)	1	1
32	—	6	20 (10)	20 (9)	15 (4)	15 (4)	1	1
35	—	6 (2)	21 (9)	21 (10)	16 (8)	16 (8)	2	2
39	—	6 (3)	20 (10)	20 (9)	16 (7)	16 (7)	2	2
44	female	6 (3)	21 (11)	22 (9)	18 (7)	19 (7)	4	5
49	male	6 (3)	20 (8)	20 (8)	18 (8)	20 (10)	3	3
55	female	6 (2)	19 (8)	19 (10)	15 (7)	15 (6)	7	8
60	female	6 (3)	19 (11)	19 (9)	16 (7)	15 (8)	2	2
65	male	6 (2)	20 (8)	20 (8)	17 (8)	17 (7)	4	4
66	female	7 (2)	18 (8)	18 (8)	15 (9)	15 (8)	3	3
67	female	6 (2)	21 (10)	20 (10)	17 (8)	17 (9)	3	3
68	female	6 (2)	21 (11)	21 (11)	17 (9)	16 (9)	2	2
70	male	6	21	20	17 (7)	17 (7)	2	4
74	male	6 (3)	21	20	16 (7)	16 (8)	2	4
78.5	male	6 (3)	20	19	17 (7)	17 (6)	1	1
79	male	6 (3)	23 (12)	23 (8)	17 (7)	17 (7)	2	2
81	male	6 (1)	19 (7)	21 (8)	18 (6)	17 (8)	2	2
88	male	6 (2)	21 (8)	20 (11)	18 (6)	18 (5)	1	1

FIGURES

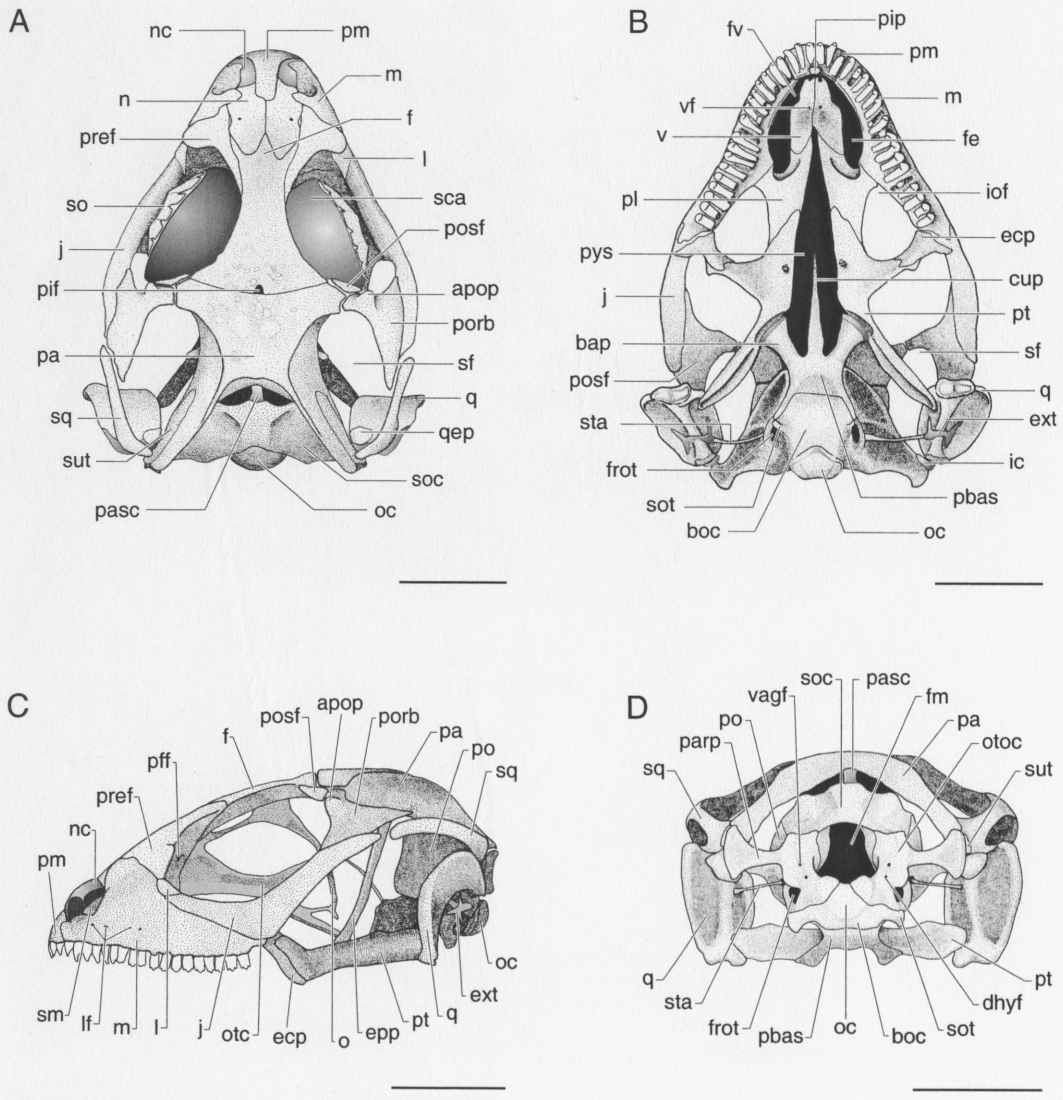

Fig. 1. *Stenocercus guentheri*. Skull of adult (**A**, **B**, **C**, KU 147412; **D** KU 147319) in dorsal (**A**), ventral (**B**), lateral (**C**) and posterior (**D**) views. apop, anterodorsal postorbital process; bap, basipterygoid process; boc, basioccipital; cup, cultriform process; dhyf, dorsal hypoglossal foramen; ecp, ectopterygoid; epp, epipterygoid; ext, extracolumella; f, frontal; fe, fenestra exochoanalis; fm, foramen magnum; frot, foramen rotundum; fv, fenestra vomeronasalis externa; ic, intercalary cartilage; iof, inferior orbital fenestra; j, jugal; l, lacrimal; lf, labial foramina; m, maxilla; n, nasal; nc, nasal cartilages; o, orbitosphenoid; oc, occipital condyle; otc, orbitotemporal cartilages; otoc, otoccipital; pa, parietal; parp, paraoccipital process; pasc, processus ascendens; pbas, parabasisphenoid; pff, prefrontal foramen; pif, pineal foramen; pip, posteromedial incisive process; pl, palatine; pm, premaxilla; po, prootic; porb, postorbital; posf, postfrontal; pref, prefrontal; pt, pterygoid; pys, pyriform space; q, quadrate; qep, quadrate epiphysis; sca, sclerical cartilage; sf, supratemporal fossa; sm, septomaxilla; so, scleral ossicles; soc, supraoccipital; sot, sphenoccipital tubercle; sq, squamosal; sta, stapes; sut, supratemporal; v, vomer; vagf, vagal foramen; vf, vomerine foramen. Gray indicates cartilage; stippled gray denotes calcification. Scale bars = 5 mm.

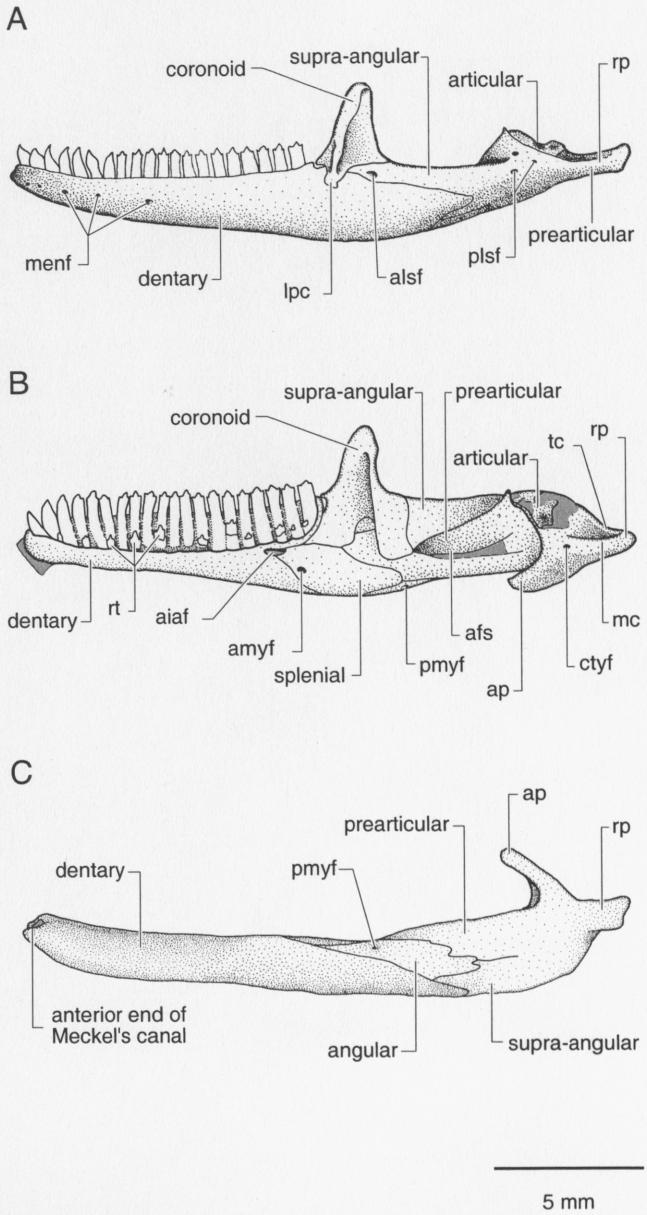

Fig. 2. *Stenocercus guentheri*. Mandible of adult (KU 147412) in lateral (**A**), medial (**B**), and ventral (**C**) views. afs, adductor fossa; aiaf, anterior inferior alveolar foramen; alsf, anterolateral supra-angular foramen; amyf, anterior mylohyoid foramen; ap, angular process; ctyf, chorda tympani foramen; lpc, labial process; mc, medial crest; menf, mental foramina; plsf, posterolateral supra-angular foramina; pmyf, posterior mylohyoid foramen; rp, retroarticular process; rt, replacementh teeth; tc, tympanic crest. Gray indicates Meckel's cartilage.

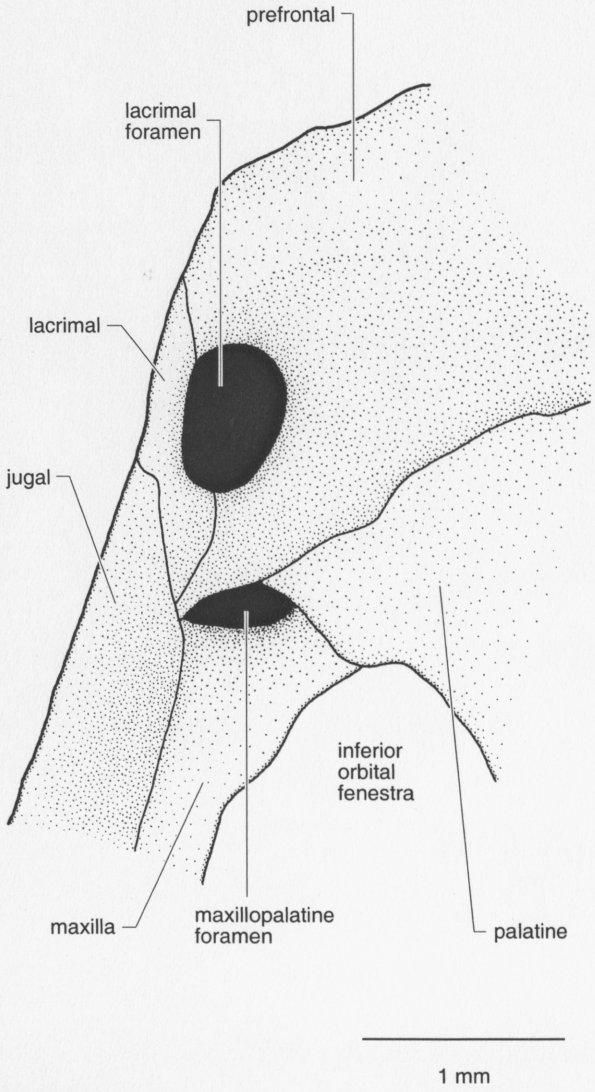

Fig. 3. *Stenocercus guentheri*. Anterior margin of orbit of adult (KU 147326) in posterior view.

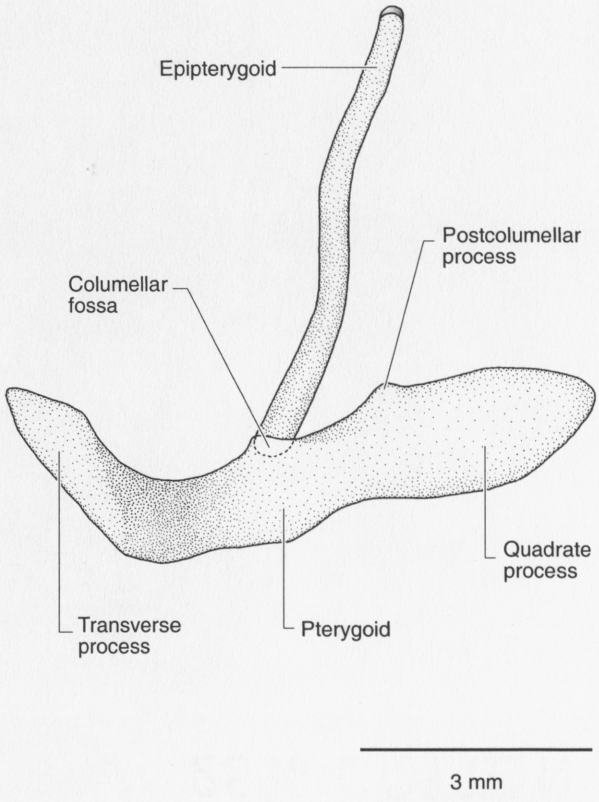

Fig. 4. *Stenocercus guentheri*. Left pterygoid and epipterygoid of adult (KU 147326) in lateral view. Gray denotes cartilage.

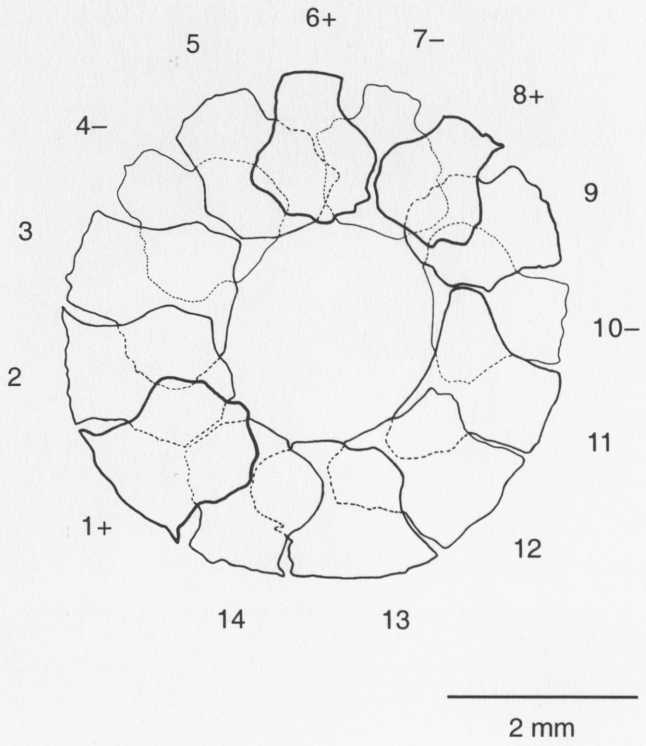

Fig. 5. *Stenocercus guentheri*. Right scleral ossicles of adult (KU 147412) in lateral view. "+" denotes ossicles overlapping both neighbors, "–" denotes ossicles overlapped by both neighbors.

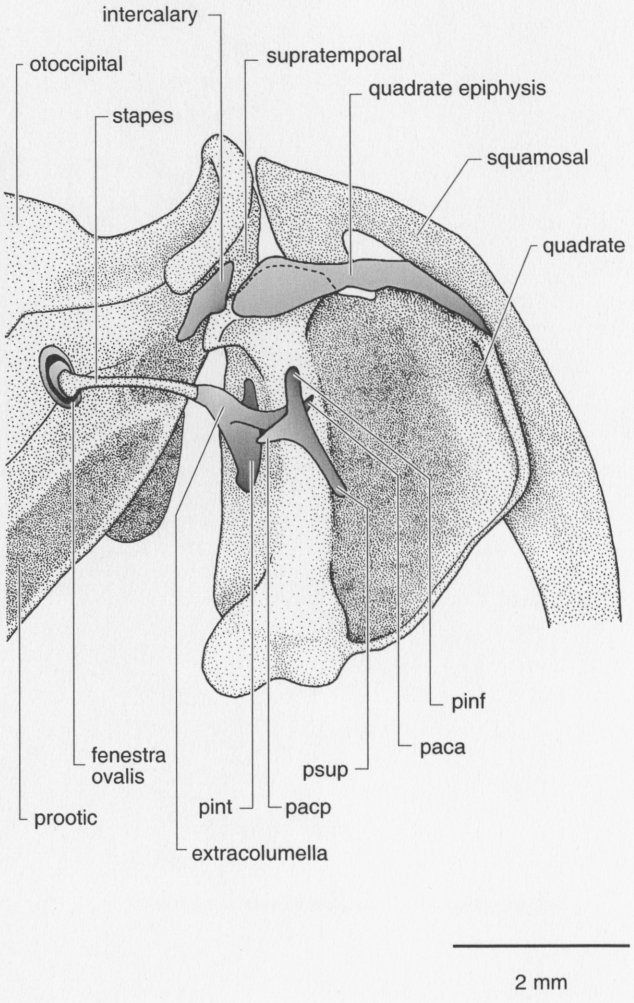

Fig. 6. *Stenocercus guentheri*. Right middle ear of adult (KU 147412) in posteroventral view. paca, processus accesorius anterior; pacp, processus accesorius posterior; pinf, pars inferior; pint, processus internus; psup, pars superior. Gray represents cartilage.

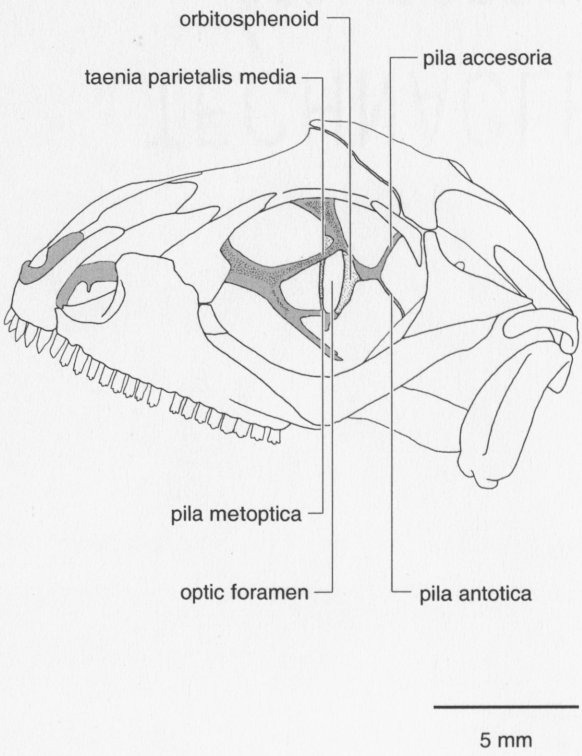

Fig. 7. *Stenocercus guentheri*. Orbitotemporal region of adult (KU 147412). Gray and stippled gray denote cartilage and calcified cartilage, respectively.

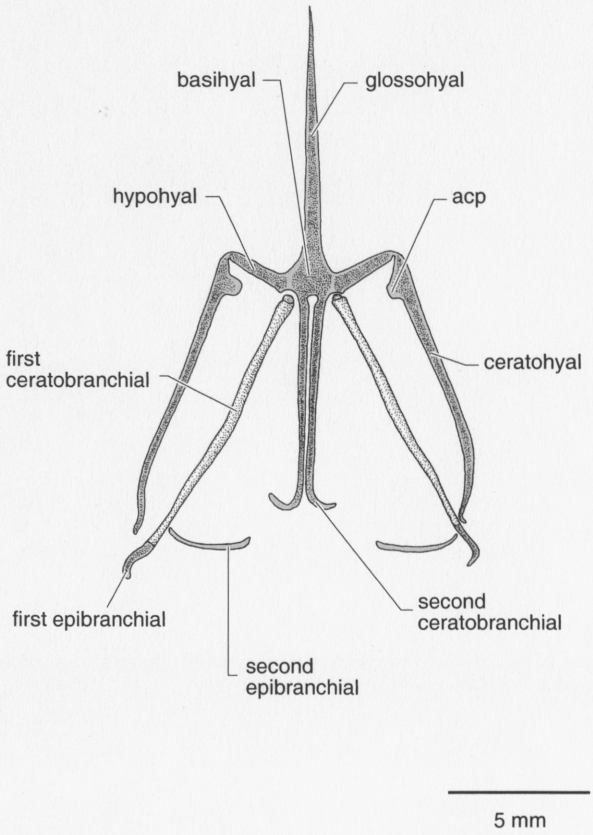

Fig. 8. *Stenocercus guentheri*. Hyoid apparatus of adult (KU 147412) in ventral view. acp, anteromedial ceratohyal process. Gray and stippled gray denote cartilage and calcified cartilage, respectively.

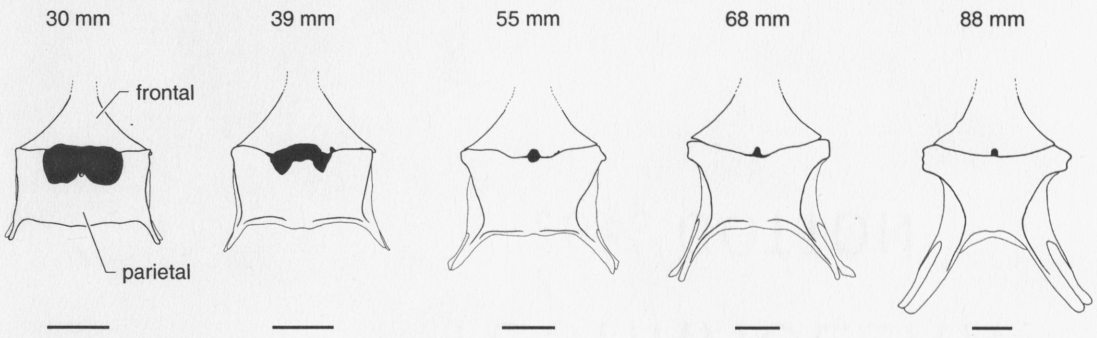

Fig. 9. Outline drawings of development of the parietal of *Stenocercus guentheri* in dorsal view. Numbers above indicate SVL of the specimen illustrated. Black represents the frontoparietal fontanelle. Scale bars = 2 mm.

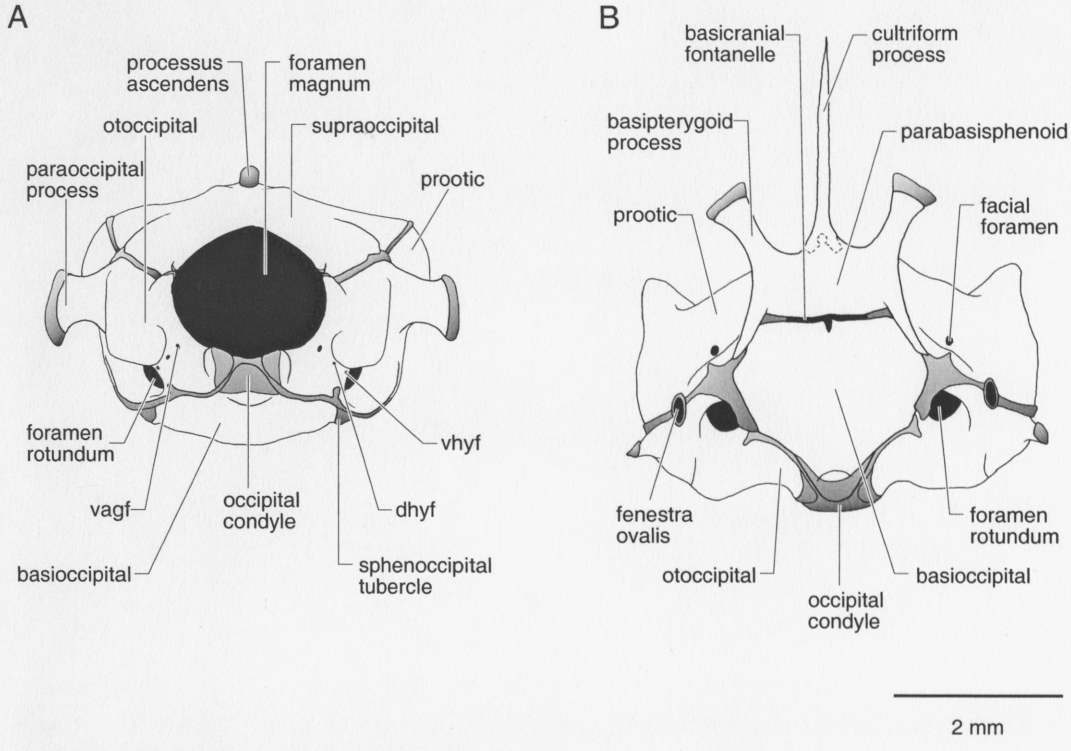

Fig. 10. *Stenocercus guentheri*. Neurocranium of juvenile (KU 147347) in posterior (**A**) and ventral (**B**) views. dhyf, dorsal hypoglossal foramen; vagf, vagal foramen; vhyf, ventral hypoglossal foramen. Gray indicates cartilage.

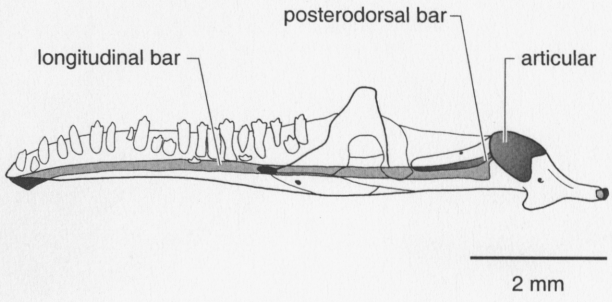

Fig. 11. *Stenocercus guentheri*. Meckel's cartilage of juvenile (KU 147347) in medial view. Exposed areas are shown in dark gray.

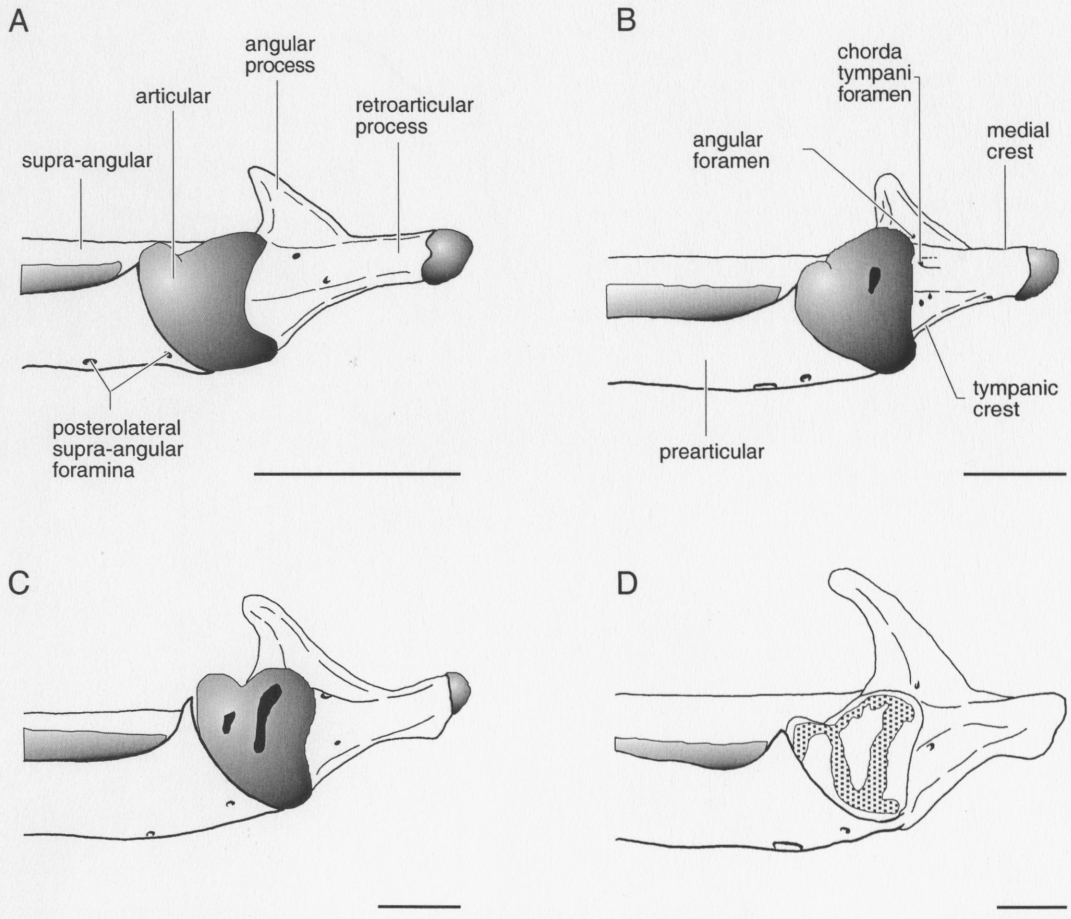

Fig. 12. *Stenocercus guentheri*. Dorsal view of the posterior aspect of the mandible of four specimens: KU 147347, 30 mm SVL (**A**); KU 147445, 55 mm SVL (**B**); KU 147409, 65 mm SVL (**C**); KU 147412, 88 mm SVL (**D**). Stippling indicates calcified cartilage, gray represents cartilage, and black denotes centers of ossification of articular. Scale bars = 2 mm.